Aspects of the ecology of Weddell seals at the Vestfold Hills, Prydz Bay, East Antarctica

by

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(Samantha E. Lake)

Table of Contents

Summary

At first glance, the head of a Weddell seal, *Leptonychotes weddelli*, seems small for its body. This is due to the streamline profile for swimming and breathing through holes in the ice. Ice frozen, or 'fastened', to the shore (fast-ice) surrounds the coast of Antarctica and is the Weddell seal's habitat (Kooyman 1968). Weddell seal females pup for the first time, on average, at seven years and can live to 24 years producing pups approximately annually until near the end of that time (Green *et al.* 1993). The number and timing of pups is related to the environment which changes cyclically (Testa *et al.* 1991, White and Peterson 1996). Interannual variation is currently being investigated by monitoring the population of Weddell seals at Vestfold Hills, Prydz Bay, East Antarctica

A diurnal cycle in Weddell seal haul-out behaviour has been described at McMurdo Sound, Antarctica, but prior to this thesis regional and seasonal variations in haul-out patterns of Weddell seals were unknown. Knowledge of activity patterns was required to standardise survey methods and survey data. This study examined diurnal haul-out behaviour of Weddell seals at the Vestfold Hills between October 1994 and March 1995. Sequential counts of seals on the ice showed that seal abundance differed up to 95% between 0930 and 1930 hours. Fewer seals were on the ice in the morning compared to the afternoon. Maximum numbers of seals were on the ice at the warmest time of day. The diurnal cycle was less pronounced in the breeding season than in the moulting season. The findings indicated the importance of surveying Weddell seals after 1200 hours and

before 1700 hours local time especially in the moulting season. Correction factors were given for month and time of day.

The breeding habitat of Weddell seals was investigated for information relevant to estimating Weddell seal population size by stratified surveys. The distribution of seals in the breeding season (September - November) was described for Long Fjord which was probably the most concentrated and consistent breeding site of Weddell seals in Prydz Bay, East Antarctica. The study area was 40 km^2 from the most east to most west breeding sites in the fjord. The 18 years of seal data included sightings of 3 205 adults and 2 319 pups. Seals were not randomly distributed. They mainly occupied one of four channels in the fjord. The location of breeding sites varied, probably due to interannual variation in ice-structure. Original methods to quantify ice-structure were used to investigate whether ice-structure accounted for the non-random distribution of seals as well as interannual variation in location of breeding sites. Data were preliminary but they suggested that the distribution of seals was not determined by ice-structure. Other aspects of habitat were discussed to emphasise the types of data required to describe the components of the breeding habitat of Weddell seals.

The diet of Weddell seals at the Vestfold Hills has been sampled every summer in the 1990's as part of the population monitoring program. The aim has been to describe interannual variation in diet concurrent with changes in population demographics. The study in this thesis was of variation in Weddell seal diet within years so that, if present, the variation can be controlled when making interannual comparisons of diet. In this study, Weddell seal faecal samples (n = 216) were collected from various areas at the Vestfold Hills. The collections were bi-

monthly between October 1994 and February 1995. The most common prey by frequency of occurrence were benthic fish (71%) and prawns (58%). Cephalopods (12%) were a minor component of diet in the breeding season (October - December). Pelagic fish (7%) were a minor component of the diet outside the fjords and in the moulting season (February). For the first time of any Antarctic predator *Trematomus scotti*, a common benthic fish, was detected in the diet. There was significant variation in the frequency of occurrence of the dominant prey types, both within Long Fjord and between Long Fjord and other sites. This indicated that it was necessary to control for temporal and spatial variation in Weddell seal diet to achieve precise interannual comparisons.

It is far from a trivial matter to determine changes in pinniped populations. The number of seals on top of the ice varies considerably, and if counts of seals are to be used as an index of population size then factors that affect the proportions of seals on the ice and in the water need to be controlled or corrected for. This thesis reports diurnal variation in numbers of seals and how the diurnal pattern changes seasonally (Ch. 2), but there are other variables that also need to be considered such as tidal and lunar cycles. The ultimate effect of changes in population parameters is a population increase or decrease. Surveys of population size need to be on a regional scale and Weddell seals are not randomly distributed (Ch. 3). It would be more efficient to know where seals are abundant and survey those areas intensely. At this stage, aspects of habitat that determine Weddell seal abundance are not known and more research is required to be able to predict the locations of concentrations of Weddell seals. Interannual variation in diet provides useful information for inferring the reasons for population fluctuations

and modelling potential impacts of man. Methods for collecting samples to represent Weddell seal diet accurately are discussed in Chapter 4. This will assist comparisons of diet between years in showing real changes in the Prydz Bay ecosystem and the impact on Weddell seals as top predators in that ecosystem.

Weddell seals (*Leptonychotes weddelli*)

Chapter 1. Weddell seals

1.1 Introduction

At first glance, the head of a Weddell seal, *Leptonychotes weddelli*, seems small for its body. This is due to the streamline profile for swimming and breathing through holes in the ice. Ice frozen, or 'fastened', to the shore (fast-ice) surrounds the coast of Antarctica and is the Weddell seal's habitat (Kooyman 1968). Air temperatures in winter are often below -20°C but water temperatures become no cooler than -1.8°C (the freezing point of normal seawater, Streten 1986). Weddell seals are able to live under the ice when the weather above is unfavourable. Adult Weddell seals are about three metres long and weigh 400 to 500 kilograms. Females are slightly larger than males (Stirling 1971a) which is characteristic of all four Lobodontine phocid species which inhabit Antarctic waters (Laws 1984). Weddell seal females pup for the first time, on average, at seven years and can live to 24 years producing pups approximately annually until near the end of that time (Green *et al.* 1993). The number and timing of pups is related to the environment which changes cyclically (Testa *et al.* 1991, White and Peterson 1996). The greatest seasonal and interannual variability in East Antarctic ice coverage tends to occur in Prydz Bay (Lenke *et al.* 1980, Allison 1989). Interannual variability in the Prydz Bay ecosystem is currently being investigated by monitoring the population of Weddell seals at Vestfold Hills, Prydz Bay, Antarctica.

1.2 Habitat

The Antarctic environment has pronounced variation in solar radiation that results in extreme seasonality of climate (Kirkwood 1993). The seasonal changes in hours of daylight result in a pulse of production in summer (Laws 1994) that is related to melting of the sea-ice and release of sympagic organisms. Warm-blooded animals depend on sea-ice as a platform, and the organisms living within or beneath the sea-ice provide a substantial part of total primary production (Spindler 1994). Sea-ice cover increases from 4 000 000 km2 in summer to 20 000 000 km2 in winter (Zwally *et al.* 1983, Parkinson *et al.* 1987). Sea-ice starts to form in autumn when the air is still and the water surface chills below freezing point. Fine ice crystals form and thicken to sludge which hardens to thin ice within 24 hours. Wind and swell break the ice sheet into floes but where the climate is very cool the ice floes reconcile to a sheet of ice on top of the water. The sheet of ice is called fast-ice. Unconsolidated floes further north are called pack-ice. The pack-ice is a floating home for crabeater seals, *Lobodon carcinophagus* (7 000 000 animals), leopard seals, *Hydrurga leptonyx* (300 000 animals) and Ross seals, *Ommatophoca rossii* (130 000 animals). The fast-ice is the more stable home of Weddell seals (800 000 animals) (Laws 1984, Erickson and Hanson 1990). This highly specialised niche offers Weddell seals protection from predators (such as killer whales, *Orcinus orca*, and leopard seals) and minimal competition for food. However, the fast-ice niche requires special skills in an air-breathing mammal.

When Weddell seals are in the water they breathe through breaks in the fast-ice or at areas of open water such as polynyas. Weddell seals also use breaks in the ice to haul-out of the water and rest on the ice. Cracks in the ice form inshore because of tidal movement which lifts and drops the level of the ice and makes rifts (called tide-cracks) where the fast-ice is frozen to stable bodies such as land or ice-bergs (Stirling 1969a). Glacial advance also causes cracks to form in the fast-ice by pushing the sea-ice away from the shores (Stirling 1969a). In spring and summer these forces are sufficient to crack the ice. In winter, when fast-ice grows to several metres thick, neither force is sufficient to break the ice for seals to emerge. Seals can breathe at cracks and use their canine teeth to 'core' holes when the cracks refreeze, or they can move further offshore to rifts of open water. Tooth-wear from maintaining breathing holes is a major cause of adult mortality at some locations (Stirling 1971b). Most of the year, Weddell seals follow cracks and rifts in the fast-ice as it moves, retreats and advances. In Prydz Bay during winter there is ample open water, both in front of the Sörsdal Glacier (Green *et al.* 1993) and at recurrent polynyas associated with anomalously warm waters in the centre of the bay (Smith and Treguer 1994).

Weddell seals must find their way to a breathing hole before body oxygen stores are exhausted. They are very capable divers and able to dive to more than 720 m (Schreer and Testa 1996) and for up to 73 minutes (Kooyman 1981). Like most seals, Weddell seal nutrition is derived totally by diving for prey. Foraging dives are usually in bouts, each dive for approximately 20 minutes (Schreer and Testa 1996). Prydz Bay is characterised by depths near 600 m. Weddell seals are

capable of foraging in the benthos throughout at least some of their range. Dives for more than 20 minutes may be for exploration and travelling to distant breathing holes (Kooyman 1981). Swimming speeds of 1.3 m.s-1 (Ponganis *et al.* 1993) indicate that they are able to travel up to 30 km without breathing. The overall pattern of deeper dives during the daytime, and a tendency towards deeper dives during the full moon periods, suggests that vision is the most important mechanism of perception for Weddell seals (Kooyman 1981, Wartzok *et al.* 1992).

1.3 Weddell seal life cycle

The summer behaviour of Weddell seals is documented by Kooyman 1968, 1975, 1981, Stirling 1971b, Kooyman *et al.* 1983, Testa and Siniff 1987, Siniff 1991). Weddell seals, like all seals, must give birth to their pups out of water and this normally takes place on the ice. Breeding colonies assemble at tide-cracks that form in spring in securely held fast-ice. Seals begin to haul-out for pupping in September and October. Pregnant females haul-out a day or two before birthing. Most pups are born by the end of November. Maternal care (lactation) is for about six weeks which is longer than for pack-ice seals and about as long as the fast-ice is accessible and stable. The first entry of pups into the water is at about one week (Tedman and Bryden 1979, Thomas and DeMaster 1983a) and the mother swims with her pup while the pup learns to use it's flippers and climb out of the water through holes in the ice. When food is abundant, lactating females eat, otherwise they may fast for two months in the breeding season (Siniff *et al.* 1977).

Males defend aquatic 'territories' around ice holes. Fighting is apparent from wounds around the males' bellies. This and other evidence suggests that Weddell seals are polygynous (Ray 1967, Bartish *et al.* 1992).

Weaning and mating are in December, when the number of seals in breeding areas are at a maximum. Fast-ice at this time has many openings for pups to use as they learn to dive and navigate. Pups stay inshore and consume crustaceans in the plankton "bloom" that occurs after the ice breaks out when the water-column is mixed by wind and illuminated by light. Remnants of inshore fast-ice are used for platforms to haul-out on and protection from predators looking for inexperienced pups. Early break-up of the fast-ice may reduce the survival of pups (Thomas and DeMaster 1983b).

Weddell seals moult at the end of summer. They do not stay on land while they moult but higher skin temperatures achieved by hauling out do allow the moult to proceed more rapidly. Extensive melting of the fast-ice close to land reduces the resting sites for moulting seals, and so they form dense aggregations in inlets where multi-year sea-ice remains (Stirling 1969b). The hunting range and success of Weddell seals during the moulting season is not influenced by availability of breathing holes and tide-cracks, but probably more by the distribution of sea-ice (Green and Burton 1987). Weddell seals appear reluctant to leave areas of remnant fast-ice until about March or April when killer whales begin their winter migration from Antarctic waters (Testa *et al.* 1985).

The activities of the Weddell seal during winter (eight months of the year) are mostly a mystery (Davis *et al.* 1982, Green and Burton 1987, Castellini *et al.* 1992, Testa 1994, Schreer and Testa 1996). Few seals are seen on the ice but

their apparent scarcity is probably due to difficulties reaching the ice-surface and the less comfortable environment on top of the ice in winter. Their underwater calls can still be heard with hydrophones (Green and Burton 1988). Studies of Weddell seal diet and range during winter show that the seals are dispersed over a greater area than in summer. While some continue to forage near the coast, others move further across the continental shelf and make occasional journeys of several hundred kilometres into the heavy winter pack-ice (Green and Burton 1987, Testa 1994). This and other evidence (eg. Erickson and Hanson 1990) suggests that Weddell seal range is mainly limited to the continental shelf. Diving during winter is at shallower depths than in summer (Kooyman 1975, Testa 1994). A significant proportion of Weddell seal nutrition is acquired in winter (Wilson 1907, Schreer and Testa 1996) and knowledge of ecosystem interactions during winter as well as summer is necessary to understand how ocean events affect Weddell seal populations.

1.4 The ecosystem

Laws (1994) considered that there are two food webs in the Southern Ocean for higher-level predators. These are the 'oceanic zone' and the 'shelf zone'. The oceanic zone refers to the open ocean north of the continental shelf. The shelf zone (where Weddell seals occur) is over the continental shelf and characterised by the cold near-shore water-masses. Most species are confined to either one zone or the other. In the shelf zone, zooplankton biomass is low. Krill, *Euphausia*

superba, is replaced by *E. crystallorophias*. Pelagic fish, *Pleuragramma antarcticum*, is abundant and feeds mainly on *E. crystallorophias* (Hubold 1985). Most of the very intense but brief production period goes to the rich epi-benthic fauna of suspension feeders which are the food-source of crustaceans, cephalopods, and a high number of fish species. It seems that because the shelf-zone system is a long way south it has brief outbursts of primary productivity that cannot sustain a rich pelagic food web but only a community of benthic feeders which exploit detritus concentrations. Benthic organisms do not use energy for swimming and survive periods of starvation at negligible metabolic cost (Hempel 1985).

The oceanic and shelf zone ecosystems do interact. Features such as Prydz Bay cause eddies in the circular current system around the Southern Ocean (Smith and Treguer 1994). Circulation within the bay is characterised by a clockwise gyre fed by a broad inflow from the northeast, and a stronger coastally-confined outflow toward the west. This connects the shelf waters with oceanic waters (Smith and Treguer 1994). On a larger scale, the Southern Ocean is the unifying link for exchange of water masses between the world's ocean basins (White and Peterson 1996). The Southern Ocean is subject to both natural and anthropogenic influences. There is a major, short-term (approximately 4 year) climatic periodicity around Antarctica referred to as the Antarctic Circumpolar Wave (ACW) (White and Peterson 1996). Evidence from oceanographic relationships between sea-surface-temperature, sea-surface-air-pressure, sea-height and wind-vectors show that very different water masses are likely to exist in areas during peaks and troughs of the ACW. In each phase of the ACW it is predictable

that species higher in the food chain will have different diets both in terms of prey species and prey abundance (Priddle *et al.* 1988). There have been fisheries in the vicinity of Prydz Bay and there is potential for more (Williams 1985). Quantification of responses of predators to natural fluctuations in the marine environment will enable modelling the response of predators to new fluctuations of anthropogenic origins superimposed on the existing cycle (Croxall 1989).

1.5 Population monitoring

The responses of Weddell seals to environmental change at the Vestfold Hills have been investigated by annual tagging and resighting of Weddell seals since 1973. Similarly, Weddell seals have been tagged and resighted at McMurdo Sound and Signy Island (Croxall and Hiby 1983, Testa *et al.* 1990). Seals at McMurdo Sound have undergone fluctuations in reproductive rate every 4 - 6 years. Comparisons with populations at Signy Island and the Vestfold Hills suggest that fluctuations are synchronous at Signy Island and McMurdo Sound but not at the Vestfold Hills. However, sampling intensity was higher at McMurdo than at other sites and when lower sampling intensity was simulated for data from McMurdo Sound there were no differences in parameters (Testa *et al.* 1990).

Fluctuations in reproductive rate are most likely energetically mediated and related to food availability over winter. Possible causes of changes in food availability include variation in the fast-ice (Stirling and Greenwood 1972), large-scale fluctuations in populations of major prey species (Green and Johnson 1988, Whitehead *et al.* 1990), or changes in ocean circulation that might affect the movement of pelagic fish (Priddle *et al.* 1988). Descriptions of interannual variation in the diet concurrent with changes in demographics show whether changes in food availability in the ecosystem are reflected by Weddell seal reproductive rate for example. This type of research is comparative and thus knowledge of variables within demographic parameters and diet are relevant for precision of data. This thesis is an attempt to provide information regarding potential variables within parameters by investigating fine-scale temporal and spatial variation in some of the parameters that have been monitored as part of the Australian Antarctic Division Weddell seal project. As such it is a logical further investigation within that program.

Weddell seals hauled out on fast-ice in summer

Chapter 2. Influence of time and month on haul-out patterns of Weddell seals

2.1 Introduction

Weddell seals (*Leptonychotes weddelli*) are only visible for surveying when they are hauled out on the ice or land. Such counts provide an index of population size that varies in relation to the total number of individuals and the proportion of the population in the water. Because survey counts are an index, precision rather than accuracy is critical for temporal and spatial comparison of counts. Precision is increased by standardisation of survey methods (Caughley and Sinclair 1994). Knowledge of haul-out patterns is required to standardise survey methods for seals (Erickson *et al.* 1989).

The haul-out activity of seals is known to vary seasonally eg. elephant seals, *Mirounga leonina* (Hindell and Burton 1988) and diurnally eg. Weddell seals (Siniff *et al.* 1971), crabeater seals, *Lobodon carcinophagus* (Erickson and Hanson 1990); and common seals, *Phoca vitulina* (Thompson and Harwood 1990). The haul-out pattern of Weddell seals is recorded by radio telemetry (Siniff *et al.* 1971; Thomas and DeMaster 1983a) or sequential counts of seals on the ice (Tedman and Bryden 1979). These studies show that few Weddell seals haul-out in the morning and maximum numbers of seals haul-out in the afternoon. However, there are few studies of Weddell seal haul-out activity outside the

breeding season (Smith 1965, Kooyman 1975) or at locations other than McMurdo Sound (Erickson *et al.* 1989). This study quantifies Weddell seal haul-out behaviour through the breeding and moulting seasons at Vestfold Hills, Antarctica. The aim is to describe appropriate survey methods and correction factors for the diurnal patterns in Weddell seal haul-out behaviour.

2.2 Methods

Experimental design and data

Weddell seals at the Vestfold Hills aggregated in colonies in the breeding season (October to December) mainly in Long Fjord. They hauled out on remnant fast-ice in the moulting season (January to March) in Tryne Fjord, Tryne Bay and Ellis Fjord (Fig 2.1). Composition of the observed herds was described by conducting surveys of tagged seals late in the afternoon every few days during the breeding season in addition to counts of seals to document diurnal haul-out behaviour. The proportion of pups born was the number of pups sighted at the date of survey compared to the maximum number of tagged pups. The proportion of pups weaned was the number of tagged pups sighted with or without attending mothers.

Diurnal variation in haul-out activity was described by counts of seals in aggregations convenient to view from the top of a hill and of sufficient number (> 20 seals) to make a reasonable sample. Three breeding colonies about 2 km apart in Long Fjord were observed from separate sites and six moulting groups in Tryne Bay were observed from one site (Fig 2.1). Observation sets were for seven days every six weeks from October to March (Table 2.1). Counts were at 150-min

intervals between 0700 and 1930 hours in the breeding season and 60-min intervals in all daylight hours in the moulting season. Pups were included in December, when the pups were swimming, but not in October when pups were new-born and not swimming. Wind speed categories (calibrated using an anemometer) and cloud cover (octas) were recorded at the sites with each count. Weather data was also obtained from the Bureau of Meteorology at nearby Davis Station.

Table 2.1 Date, location, frequency, and other information about the four sets of counts of seals on the ice. Mean and standard deviation (in brackets) are shown for weather

Date	Location	Counts per day	Interval (mins)	Study sites	Wind speed (kts)	Air temp. (°C)
19 - 25 Oct 94	Long Fjord	6	150	3	9.3 (4.1)	-11.3 (2.6)
7 - 13 Dec 94	Long Fjord	6	150	3	14.9 (6.3)	-1.2 (0.9)
20 - 26 Jan 95	Tryne Bay	24	60	1	13.1 (7.3)	-0.9 (1.4)
2 - 8 March 95	Tryne Bay	17	60	1	11.9 (4.5)	-8.0 (2.4)

Counts of seals were expressed as a proportion of the maximum number of seals counted during each 7-days period. This eliminated differences between months in the number of seals in the study area. Thompson and Harwood (1990) expressed haul-out data as a proportion of the maximum number of seals counted each day and then as average proportions for each time of day over several days. This method did not illustrate the variation between days especially at the time/s of day when maximum (100%) of seals were hauled out. The method did adjust the data to average, rather than absolute, maximum number of seals. Thus the methods of Thompson and Harwood (1990) were used to calculate the correction factors only.

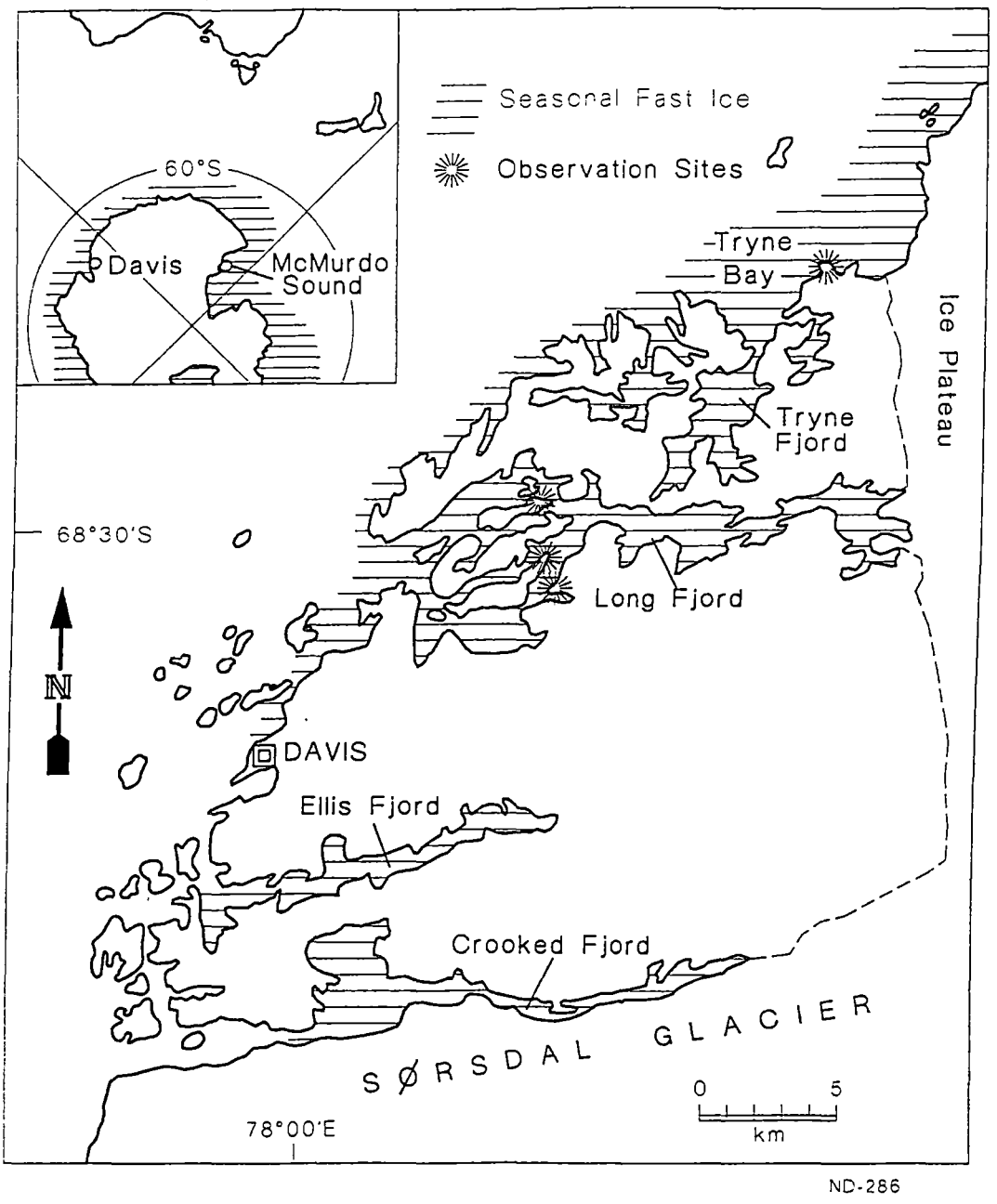


Fig 2.1 Observation sites at the Vestfold Hills in Long Fjord (three sites above breeding colonies) and in Tryne Bay (one site over-looking six aggregations of moulting seals). Also shown is the extent of the fast-ice in summer. In spring the extent of fast-ice is many kilometres from the coast.

Diurnal and seasonal analyses

The first analysis tested whether the proportion of seals on top of the ice varied significantly with time of day and if that changed in different seasons. A two-way analysis of variance was used with time of day and month of observation as the factors and the proportion of seals as the dependent variable. The number of counts per day was standardised between months to 150-min intervals between 0700 and 1930 hours. Tests for normality of the data indicated transformation was not necessary. Further analyses within months were by one-way analysis of variance with Tukey tests to investigate differences between times of day.

Weather analyses

These analyses investigated whether variation in the number of seals hauled out could be attributed to weather. Two types of analyses were run. Wind strength at the observation site was categorised as light (0 - 10 kts), moderate (10 - 23 kts) and strong (23 + kts). Counts of seals recorded in each wind condition were averaged and plotted over time of day for each month. Tests for differences were by one-way analysis of variance where number of seals was expressed as percent deviation from the mean number of seals at each time of day. The second analysis of weather was the weather data recorded at Davis station regressed with direct counts of seals for each month. The seal data were counts at times of day when average counts of seals were not significantly different and when the majority of seals were hauled out.

2.3 Results

Composition of groups

Pupping in the breeding colonies began on the first of October and rate of pupping was maximal at the end of October when 3% of total pup production (164 pups) were born each day (Fig 2.2). At the end of November the numbers of pups with attending mothers decreased rapidly (6% fewer mothers each day) and indicated onset of weaning. The first observation set was at the time of maximum rates of pupping and the second observation set was just before the time of weaning (Fig 2.2). The ratio of female to male adult seals in October was 86%, in December was 77%, in January was 38% and in March was 60% female. The maximum number of seals counted in October was 68 (pups excluded), in December 84 (pups included), in January 132 and in March 113 seals.

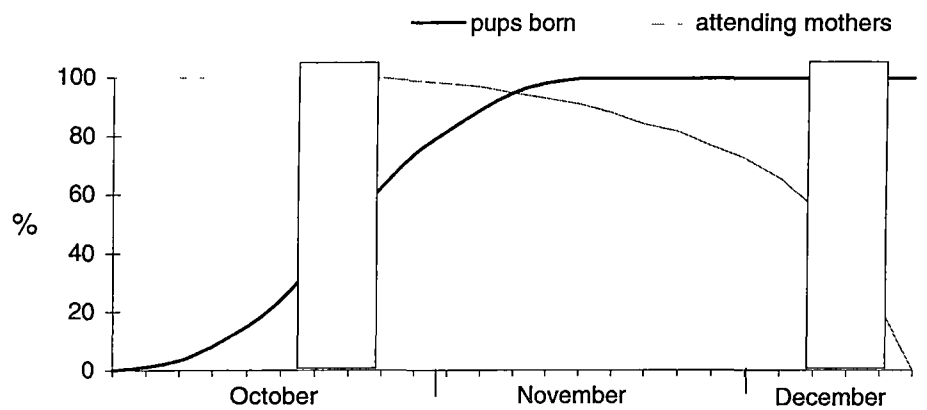


Fig 2.2 Dates of haul-out observations (bars) in the breeding season in relation to proportion of pups born and pups weaned and thus composition of the seal herds observed for diurnal activity

Seasonal changes in haul-out activity

The proportion of seals hauled out was significantly higher in October (70 ± 17%) and significantly lower in March (31 ± 26%) than in December (62 ± 21%) or January (53 ± 26%) (averaged over all times of day, two-way analysis of variance $F_{3,164} = 22.50$; $p < 0.0005$) (Fig 2.3). There was also a significant interaction effect between time of day and month of observation (two-way analysis of variance $F_{15,144} = 2.66$; $p = 0.001$). For example, the greatest proportion of seals on the ice was at 1200 hours in October and 1700 hours in March (Fig 2.3).

Diurnal pattern in haul-out activity

The proportion of seals hauled out varied significantly with time of day (averaged over all months, two-way analysis of variance $F_{5,162} = 12.07$; $p < 0.05$). Comparisons by Tukey tests showed the relative number of seals at 0700 hours (30 ± 26%) was significantly lower ($p < 0.05$) than at 1200 hours (59 ± 23%), 1430 hours (67 ± 19%), 1700 hours (70 ± 21%) and 1930 hours (59 ± 24%). The relative number of seals at 0930 hours (42 ± 28%) was also lower than in the afternoon ($p = 0.07$, < 0.05, < 0.05, and $= 0.05$ respectively). Significance of differences between times of day were shown specifically within months in Fig 2.3.

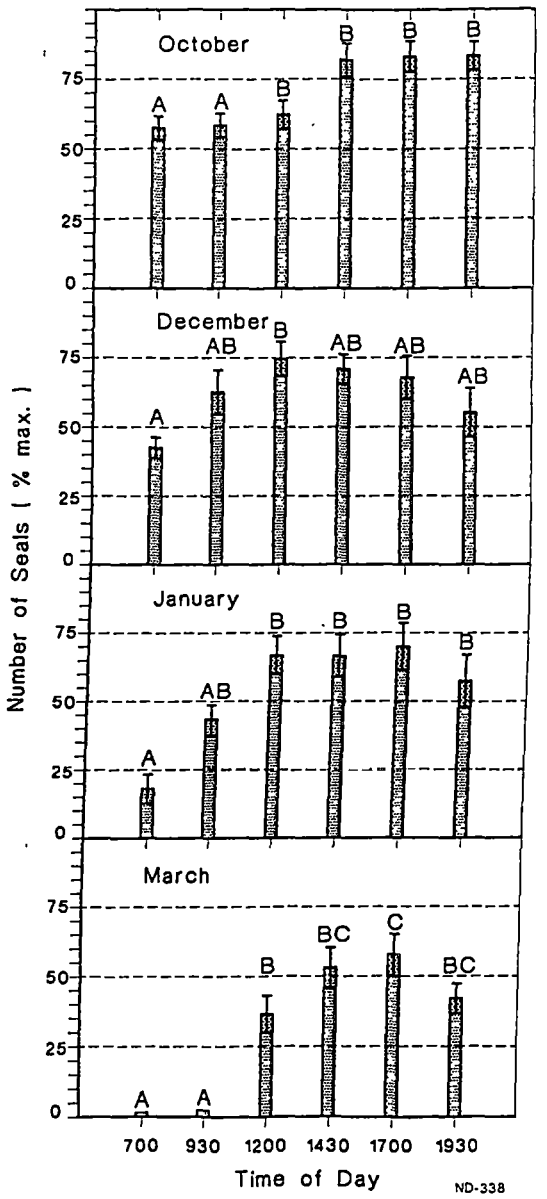


Fig 2.3 The relative number of seals hauled out (average and standard error of four sets of 7- days of counts, expressed as a proportion of the maximum number of seals counted in each 7-day period). The average numbers of seals were not significantly different where columns have been labelled with the same letters.

Weather effects

Air temperature varied significantly with time of day (one-way analysis of variance $F_7 = 22.25$, $p < 0.05$). The oscillation over 24 hours correlated with the proportion of Weddell seals hauled out: Maximum numbers of seals were hauled out at the warmest time of day (Fig 2.4). Air temperature and direct counts of seals were significantly related in December ($r^2 = 0.05$, $F_{1, 33} = 4.08$, $p = 0.05$), January ($r^2 = 0.12$, $F_{1,44} = 5.98$, $p < 0.05$) and March ($r^2 = 0.12$, $F_{1, 31} = 4.105$, $p = 0.05$) though r^2 values were low.

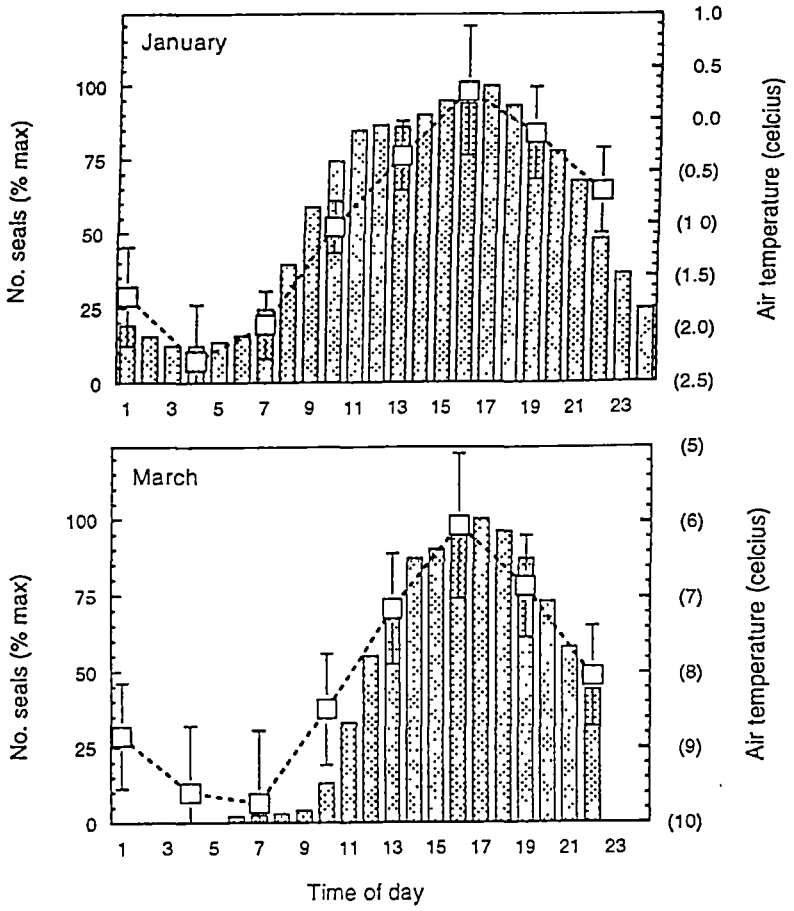


Fig 2.4 The relative number (average of 7-days) of seals hauled out in January and March (columns) shown in relation to air temperature (average and standard error of 7-days). Negative temperatures are shown in brackets.

Both analyses of wind strength (regression and analysis of variance) indicated that wind was significantly related to seal abundance in January only. Wind strength recorded at Davis Station in January was related to the number of seals hauled out ($r^2 = 0.11$, $F_{1,44} = 5.6$, $p < 0.05$). In the same month, fewer seals were hauled out in strong compared to light winds recorded at the site (one-way analysis of variance $F_{2,71} = 2.96$, $p = 0.06$) (Fig 2.5). The relationships between cloud cover and seal haul-out were not significant in any month.

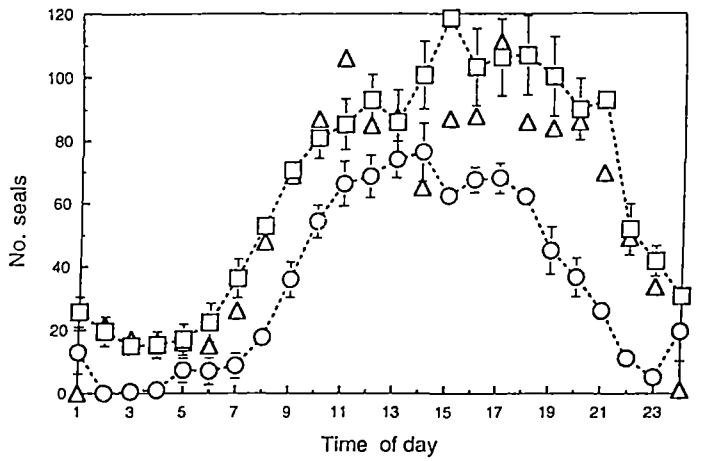


Fig 2.5 Counts of seals (average and standard error) in light (□) moderate ( ) and strong (o) winds recorded at observation sites in January.

Correction factors

Correction factors are shown in Table 2.2. Observation sets started and ended at midday in January and March. Thus the time of maximum haul-out was not monitored on the last day in those months and the number of replicates for correction factors was six not seven. Correction factors between 0900 and 1930 hours were as great as 95% at 0900 hours in March (Table 2.2).

Table 2.2 Correction factors for variation in time of day that the animals were surveyed. The values, divided into the observed number of seals, correct counts to average maximum values (1) of repeated counts (n) of numbers of seals in each month

Month	Time	Value	se	n
October	930	0.709	0.042	7
	1200	0.748	0.034	7
	1430	0.919	0.021	7
	1700	0.997	0.006	7
	1930	1.000	0.013	7
December	930	0.818	0.042	7
	1200	1.000	0.000	7
	1430	0.960	0.042	7
	1700	0.895	0.036	7
	1930	0.727	0.081	7
January	900	0.686	0.108	6
	1000	0.843	0.056	6
	1100	0.958	0.058	6
	1200	0.875	0.033	7
	1300	0.906	0.018	7
	1400	0.940	0.026	7
	1500	0.950	0.031	7
	1600	0.977	0.022	7
	1700	1.000	0.029	7
	1800	0.973	0.037	7
	1900	0.841	0.076	7
March	900	0.053	0.028	6
	1000	0.155	0.053	6
	1100	0.382	0.085	6
	1200	0.611	0.104	6
	1300	0.787	0.074	6
	1400	0.923	0.045	6
	1500	0.948	0.033	6
	1600	0.982	0.016	7
	1700	1.000	0.009	7
	1800	0.970	0.028	7
	1900	0.887	0.065	7

2.4 Discussion

This study quantified the haul-out activity of Weddell seals at the Vestfold Hills on four occasions over a 6-month period from October to March in one year.

Effect of season

A relatively large proportion of seals remained hauled out at the beginning of the breeding season in October (70%) (Fig 2.3). This was in accord with studies at McMurdo Sound (Siniff *et al.* 1971, Tedman and Bryden 1979, Thomas and DeMaster 1983a) and also with studies in the Drescher Inlet (Reijnders *et al.* 1990) at the eastern coast of the Weddell Sea. Those studies showed that haul-out activity of breeding Weddell seal females was associated with age of pups. Females hauled out for a large proportion of the time immediately after parturition and spent more time in the water from two weeks after parturition when pups started to swim. During the moulting season, the proportion of seals hauled out was relatively low (31% in March) (Fig 2.3). March was colder than the summer months (Table 2.1). Weddell seals rarely hauled out at all in winter (Green *et al.* 1993). The considerable diurnal variation in the proportion of seals hauled out in March (Fig 2.3) may have been the intermediate state between summer and winter haul-out behaviours.

Diurnal variation

Relatively few seals were hauled out in the mornings (Figs 2.3 & 2.4) as previously described for Weddell seals in McMurdo Sound (Siniff *et al.* 1971, Smith 1965, Tedman and Bryden 1979, Thomas and DeMaster 1983a). The abundance of seals on the ice was maximum post-midday in the breeding season and later in the afternoon during the moulting season (Fig 2.3). Various explanations have been given for the pattern of Weddell seal haul-out activity but none have been tested conclusively. The diurnal activity pattern may have been a response to light or air temperature (Muller-Schwarze 1965, Siniff *et al.* 1971). In this study, the haul-out pattern of seals was nearly synchronous with air temperature (Fig 2.4). When air temperature was higher at night in September, Kooyman (1975) found that more Weddell seals were hauled out at night. This suggested that Weddell seal haul-out activity was a response to air temperature and for thermoregulation rather than a response to the daylight regime.

Weather effects

Wind speed was significantly correlated with number of seals on the ice in January only. Analysis of wind speed at the study site showed that more seals were on the ice in light winds than in strong winds. At times of strong winds, the seals may have been in the water to minimise wind chill and other effects such as wind-driven snow. Similar behaviour has been reported for Weddell seals at McMurdo Sound (Smith 1965, Siniff *et al.* 1971) and elephant seals at the Vestfold Hills (Burton 1985). In this study, the absence of significant results in months other than

January suggested that wind was only one of many factors that affected haul-out. Cows with young pups stayed on the ice even in strong winds, for example. Also, conditions at Davis Station or even at the observation sites on hills above the haul-out areas, may not have been indicative of the weather conditions affecting the seals, due to lee-effects of the wind for example. More rigorous testing procedures were required to unravel the influences of environmental parameters (eg. wind) on seal activity.

Unexplained variation

There was considerable variation from day to day in the number of seals on the ice at any particular time (Fig 2.2). This was similar to other studies and accounted for by factors such as wind, air temperature, tide and season (Finley 1979, Burton 1985, Erickson *et al.* 1989, Roen and Bjorge 1995). Finley (1979) showed that a combination of bright, warm and sunny conditions during the 'night' induces ringed seals, *Phoca hispida*, to remain hauled out, but similar conditions at midday may exceed thermal tolerance and seals escaped to the water. Harrison and Kooyman (1968) noted that Weddell seals showed signs of discomfort when on the ice on sunny, windless days. Roen and Bjorge (1995) showed significant relationships between haul-out behaviour of harbour seals and tidal cycle, light cycle, and interaction of these two cycles. Thompson and Harwood (1990) showed that tidal cycle had less effect on haul-out behaviour of harbour seals in summer when strong circadian patterns were more important than in winter.

Implications for surveying

The pattern of diurnal haul-out behaviour for Weddell seals at the Vestfold Hills is the same as at other sites around the Antarctic continent (Siniff *et al.* 1971, Tedman and Bryden 1979, Thomas and DeMaster 1983a, Reijnders *et al.* 1990). Thus the conclusions from this study that apply to surveying may apply to all populations of Weddell seals. Standardisation of survey methods is not so important at the beginning of the breeding season when the majority of seals in breeding colonies are on the ice all the time. Standardisation of methods is important later in summer, especially at the end of the moulting season, when temperatures are colder and seals are on the ice for a relatively short time each day.

The proportion of seals on the ice (average for all months) is lower at 0700 hours (30%) and 0930 hours (42%) than at 1200 hours (59%), 1430 hours (67%), 1700 hours (70%) and 1930 hours (59%). Surveying between 1200 and 1930 hours, preferably between 1430 and 1700 hours, would detect maximum and comparable numbers of seals. Surveys early in the morning are underestimates of seal abundance and comparisons between morning and afternoon surveys are imprecise. Rather than discarding data collected before 1200 hours there are correction factors (Table 2.2) to express all data as maximum counts. Weather conditions and tide may provide explanations for data anomalies and should be recorded and used to determine if surveys should proceed.

Fast-ice melting near the coast at Davis Station

Chapter 3. Breeding site selection of Weddell seals in Long Fjord, Vestfold Hills

3.1 Introduction

Different methods have been used to assess the abundance of Antarctic seal species. The methods used for colonial breeding species, such as Weddell seals, are counts of pups raised by a factor related to the age structure of the population (Laws 1981). It is relevant to know the habitat of breeding Weddell seals to stratify surveying and thus allocate more census effort to areas likely to be occupied by pups. Minimum survey effort in areas unsuitable for breeding may be justified (Southwell *et al.* 1995) because the numbers of pups in these areas may be insignificant by comparison to total pup numbers.

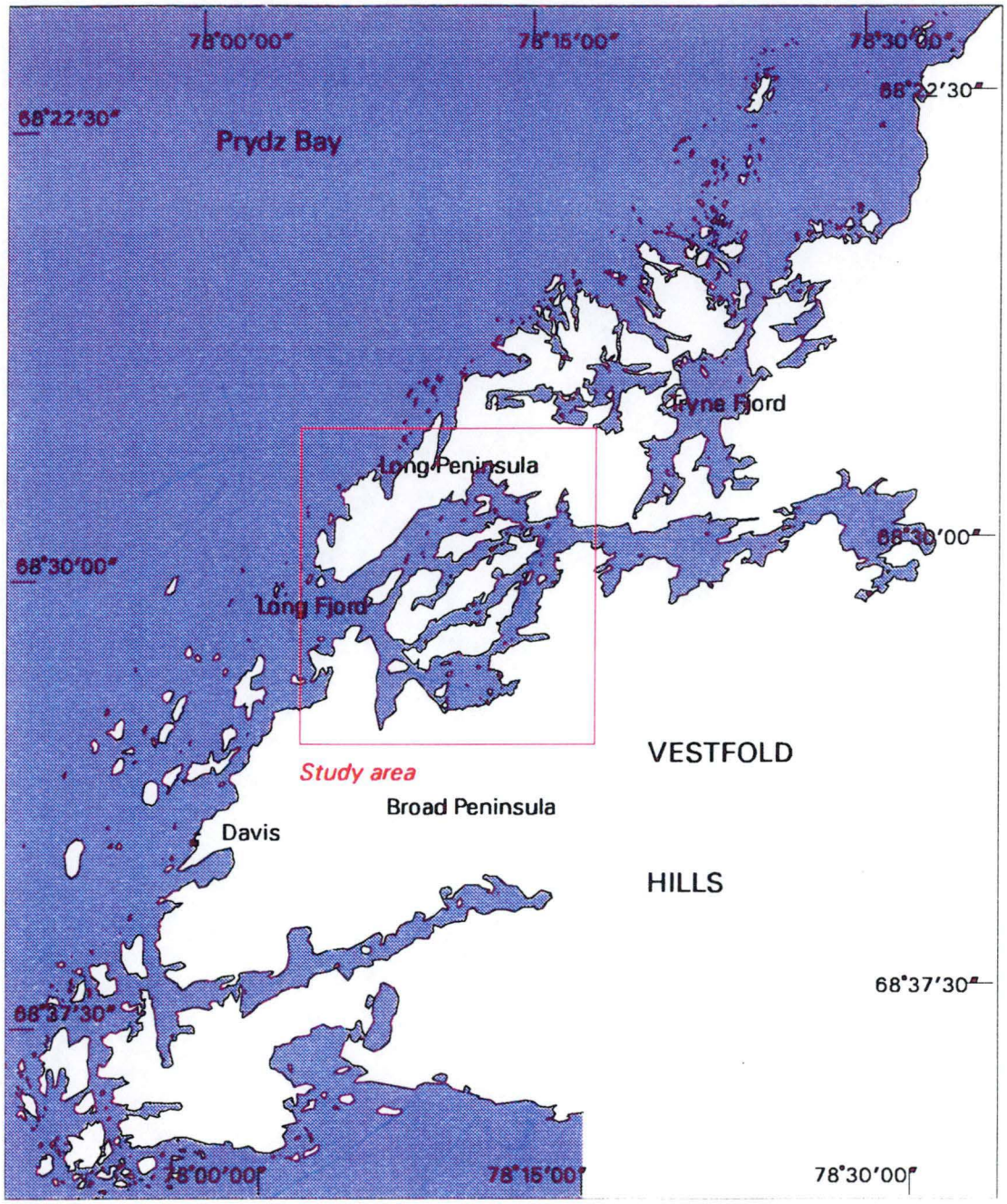
The Vestfold Hills is a 410 km^2 area of exposed continental land located on the east coast of Prydz Bay, Antarctica (68°35'S, 77°58'E). The population of Weddell seals at the Vestfold Hills is believed to be the largest breeding population of Weddell seals in Prydz Bay (Green *et al.* 1993). On average 177 pups are born each year at the Vestfold Hills. Of this, more than 100 pups each year (59%) are born in Long Fjord (Green *et al.* 1993). This makes Long Fjord an important breeding site for Weddell seals in Prydz Bay. The study describes the distribution of seals and structure of sea-ice in Long Fjord. It is the beginning of a project to more fully describe the breeding habitat of Weddell seals.

3.2 Methods

Seal distribution

The distribution of Weddell seals in Long Fjord was investigated using long-term monitoring data between 1977 and 1996. All pups born in Long Fjord were at the coastal end. The study area was defined as 63 grid squares between the furthest east and west range of the pups (Fig 3.1). Sightings were between September and November when pups were newborn. The data-base of sightings probably included most adults and all pups in the area because tag and resight effort was thorough and consistent during the study period. Only one sighting was included for each animal per season. The locations of sightings were recorded in x-y coordinates of the Burton grid-square map (1:100 000). The map defined the Vestfold Hills in grid-square dimensions 0.93 km x 0.68 km which was small enough to include whole colonies and not so coarse that two colonies would be grouped together.

Two indices of abundance were used to summarise resight data (Anderson 1993). These were number of animals, and number of years that animals, were sighted in grid-squares. Both indices were calculated for pups and adults. The category 'pups' was for animals born in each season and probably strongly reflected the distribution of pupping females. The category 'adults' was for both breeding and non-breeding animals post one-year-old and showed the distribution of all seals in the study area. The indices of seal abundance were tested for randomness by comparison of the observed distributions with Poisson distributions



Scale
1: 215,000

0 3km

Projection
Universal Transverse Mercator
Zone 44

Base mapping data courtesy of
ANARE Mapping and Geographic Information Program
Australian Antarctic Division and
Australian Surveying and Land Information Group

Produced in April 1997 for the Australian Antarctic Division,
Department of the Environment, Sport and Territories
by National Resource Information Centre,
Bureau of Resource Sciences

Fig. 3.1 Location of the study area within the Vestfold Hills, Princess Elizabeth Land, Antarctica

and tests of Chi-square goodness of fit. The data were converted from Burton grid square map to Universal Transverse Mercator projection and plotted by latitude and longitude in ARC/INFO. Grid-squares were simulated as polygons in ARC/INFO.

Ice-structure

Spatial variation of ice-structure was quantified with regard to tide-cracks and accessibility of the ice-surface to seals. Ice-structure changed with season because solar radiation between September and October increased from 10 to 20 hours per day (Streten 1986) and air-temperature increased concurrently. By the end of November the ice in Long Fjord had melted enough for cracks to widen and pools of water to flood between the cracks. By December there were large rifts of open water in the fjord. The measurements of ice-structure were made between 24 and 26 November, 1994, when melt structures were most pronounced but before they disintegrated. This was also a time of minimum tidal amplitude (http://www.ntf.flinders.edu.au./TEXT/PRJS/SOUTH/PRODS/desprods.htm/.) and thus daily variation in ice-structure was minimised.

Three aspects of ice-structure were quantified. These were height of rafting, number of cracks parallel to the shore and the degree of flooding between the cracks. Height of rafting was maximum vertical height measured in 0.5 m intervals. Number of cracks was a direct count. Amount of flooding was quantified on a subjective index from 1 - 5, where 1 was no pools, 5 was open water and intermediate scores were increasing area of flooding and thickness of ice

on the pool of water. The measurements were scored along transects through tide-cracks at right angles to the coast. Three observations were made per grid-square. Data were expressed as the maximum values recorded in each grid square. Relatedness of ice parameters was tested by multiple correlation. This was a preliminary analysis of the ice-structure data. It was conducted because it was a new type of study using original methods.

3.3 Results

Seal distribution

Over 18 years, 3 205 adults and 2 319 pups were sighted during the breeding season in 63 grid squares (Table 3.1) or 40 km^2. Assuming that each pup was associated with an adult female, 886 adults (28%) were sighted in addition to the mother-pup pairs.

Table 3.1 Summary of seal and tide-crack data showing number of grid squares (n) and minimum, maximum, mean and standard deviation of variables per grid square. Variables are numbers (n) and years of sighting (yr) of pups and adults, and the three parameters of ice-structure at coastal tide-cracks.

	Pup (n)	Adult (n)	Pup (yr)	Adult (yr)	Cracks	Flooding	Height
Grid sq. (n)	63	63	63	63	58	58	58
Minimum	0	0	0	0	3	1	1
Maximum	318	460	13	14	7	5	3
Mean	42	57	3	4	4	4	2
St. deviation	68	91	3	3	1	1	1
Total (n)	2 636	3 606	18	18	.	.	.

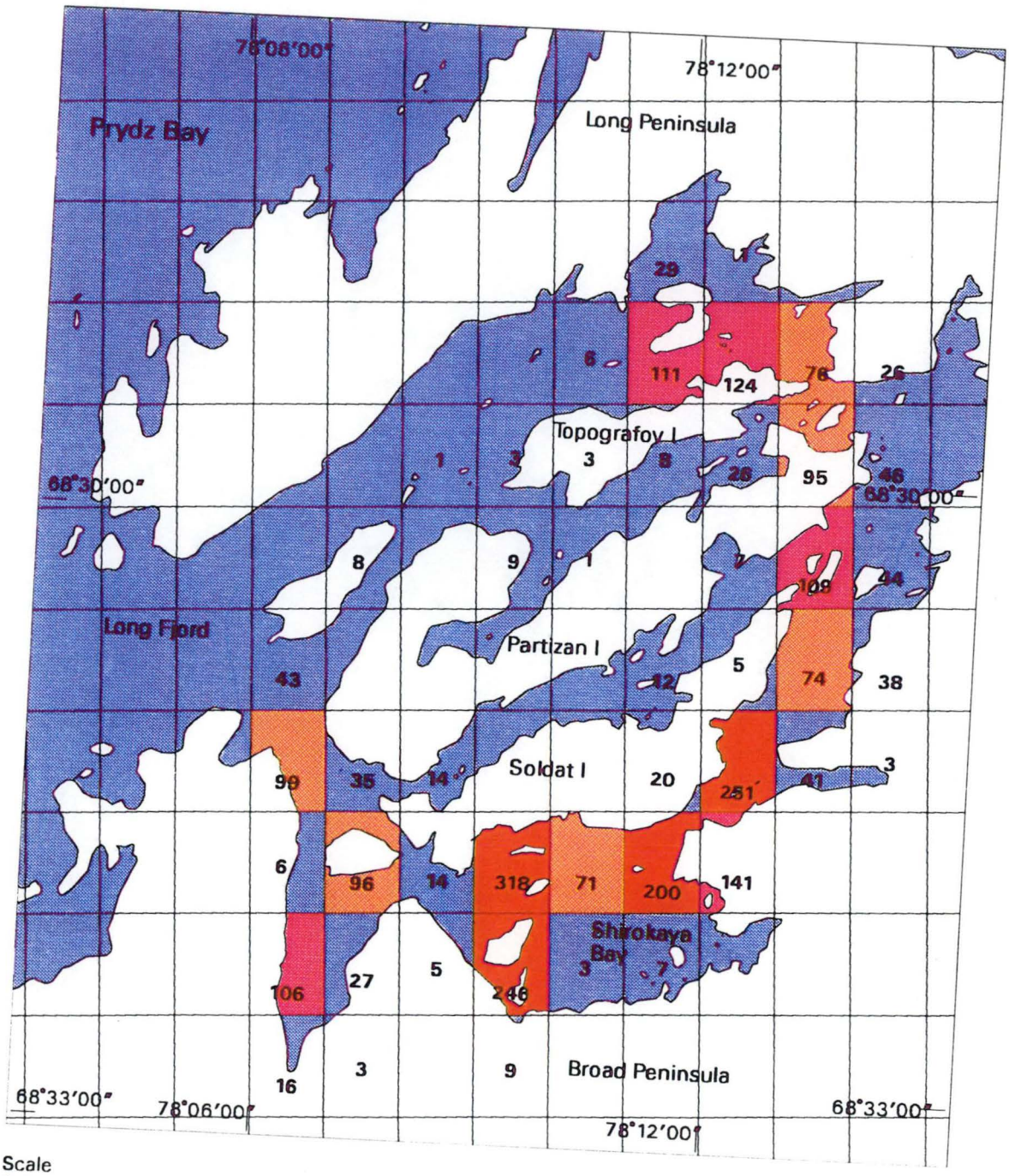


Fig. 3.2 Number of pups born in each square

Key: 50 - 100 pups; 100 - 150 pups; > 150 pups

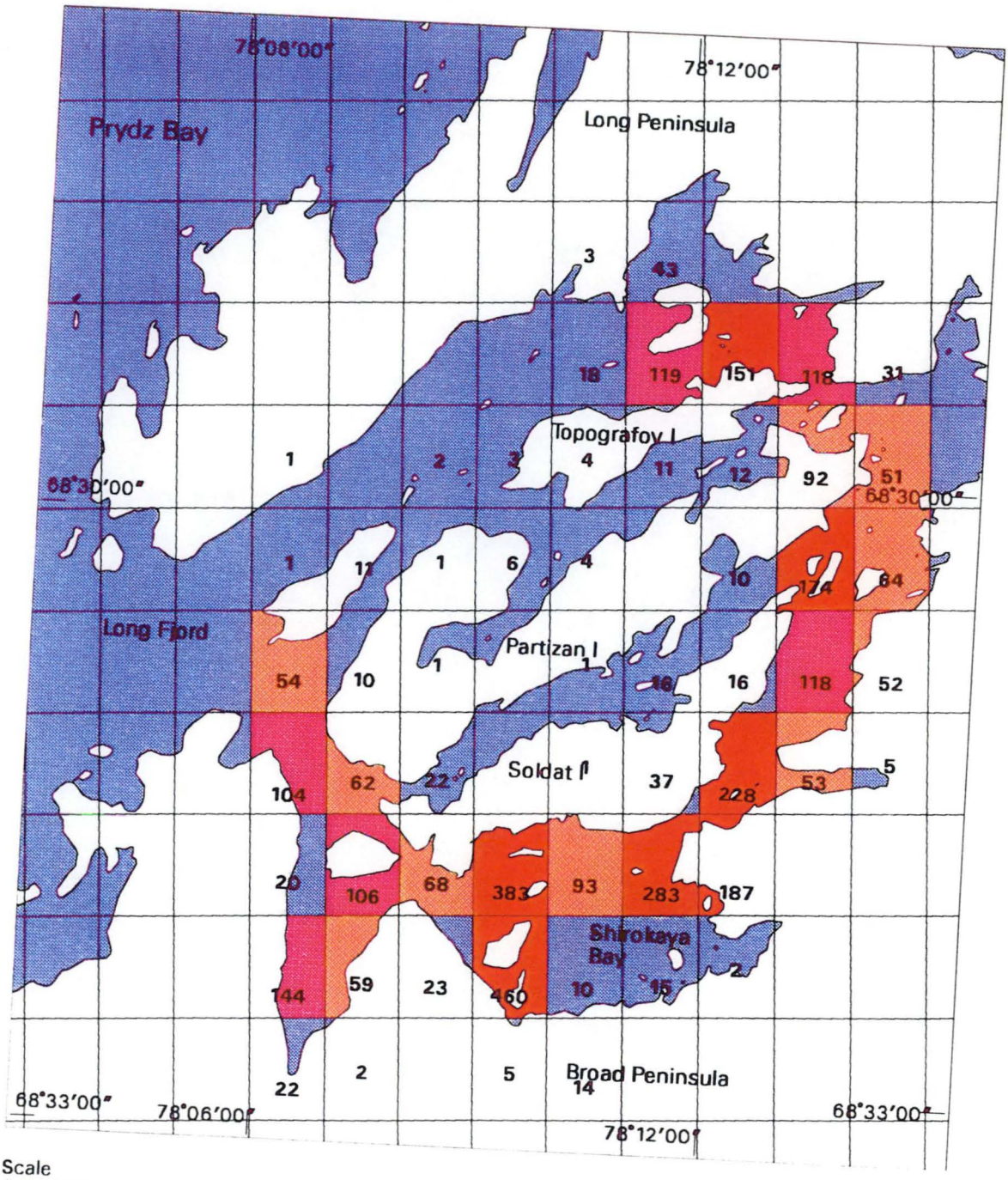


Fig. 3.3 Number of adults observed in each square

Key: 50 - 100 Adults; 100 - 150 Adults; > 150 Adults

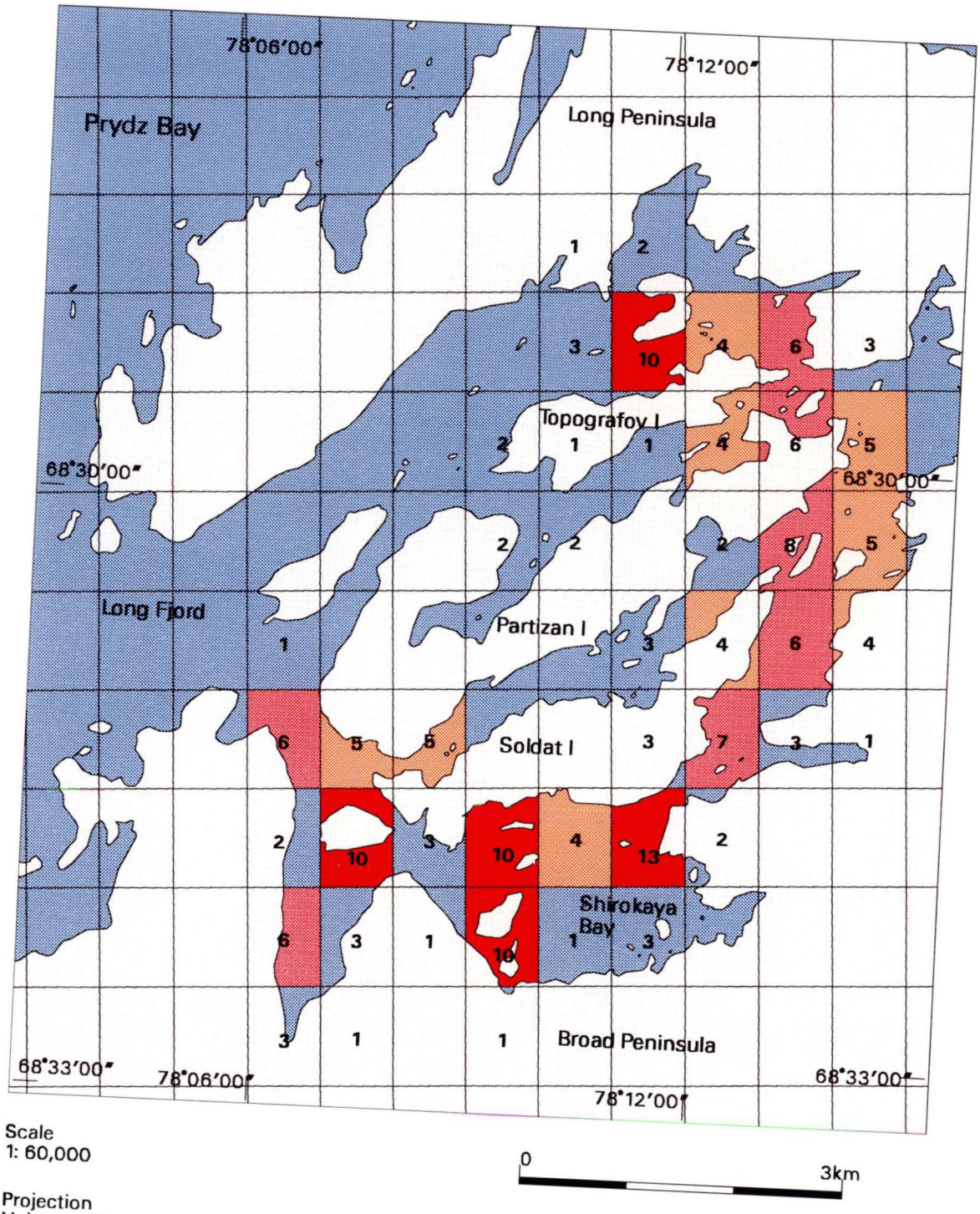


Fig. 3.4 Frequency of occupancy of each square by pups

Key: 3, 4 and 5 years; 6, 7 and 8 years; >9 years

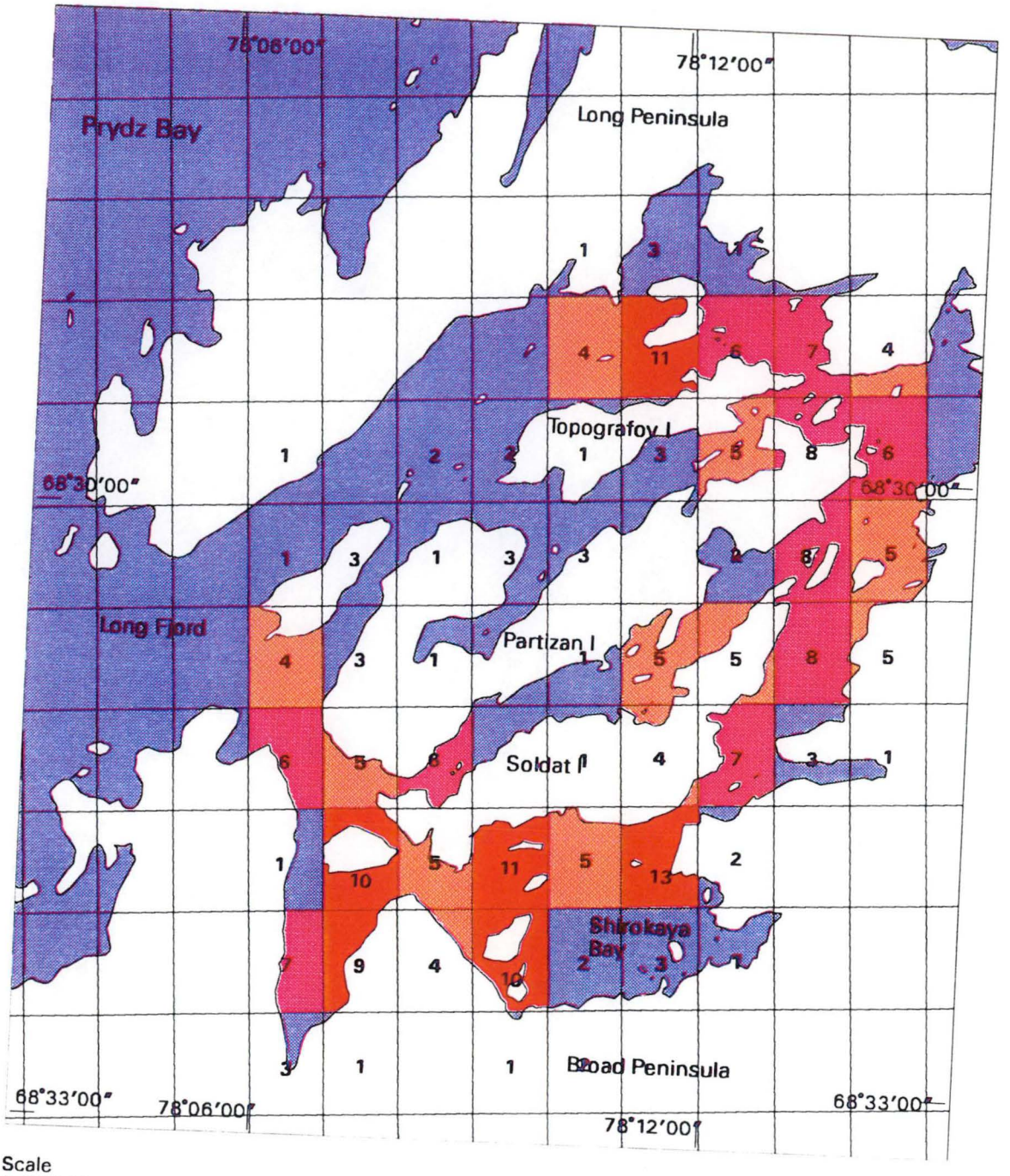


Fig. 3.5 Frequency of occupancy of each square by adults

Key: 3, 4 and 5 years; 6, 7 and 8 years; >9 years

It was evident by plotting the data (Figs 3.2 - 5) that breeding colonies were in only one of four channels in the study area. Both pup and adult sightings were concentrated in the channel from the mouth of the fjord through Shirokaya Bay and continuing north to the eastern end of the northern channel (Figs 3.2 and 3.3). Animals were seldom observed in the three other channels in study area. Only 75% of grid-squares were ever occupied by two or more seals. Maximum numbers of seals per grid square (summed over 18 years) were 318 pups and 460 adults. Mean numbers of seals per grid square were 57 adults and 42 pups (Table 3.1). Geographically, adults were distributed over a wider area than pups (Figs 3.2 and 3.3) but generally adults and pups were concentrated in similar areas.

Location of breeding colonies varied between years. The maximum frequencies of occupancy of grid squares were 13 years for pups (70%) and 14 years for adults (70%) (Table 3.1). Though breeding colonies were not located in the same grid-squares every year, the results indicated that breeding colonies were located in some grid squares for the majority of years (Figs 3.4 and 3.5).

Comparisons with Poisson distributions showed that the distributions of both pups and adults were significantly different from random. Chi-squared tests of goodness of fit with probabilities $p < 0.05$ confirmed that some grid squares were occupied significantly more often than others and by significantly higher numbers of seals (Table 3.1). The high variations around the mean values per grid square (3 ± 4 years for pups, 4 ± 3 years for adults, 36 ± 64 pups, 50 ± 86 adults per grid square) (Table 3.1) also signified non-random distribution of seals.

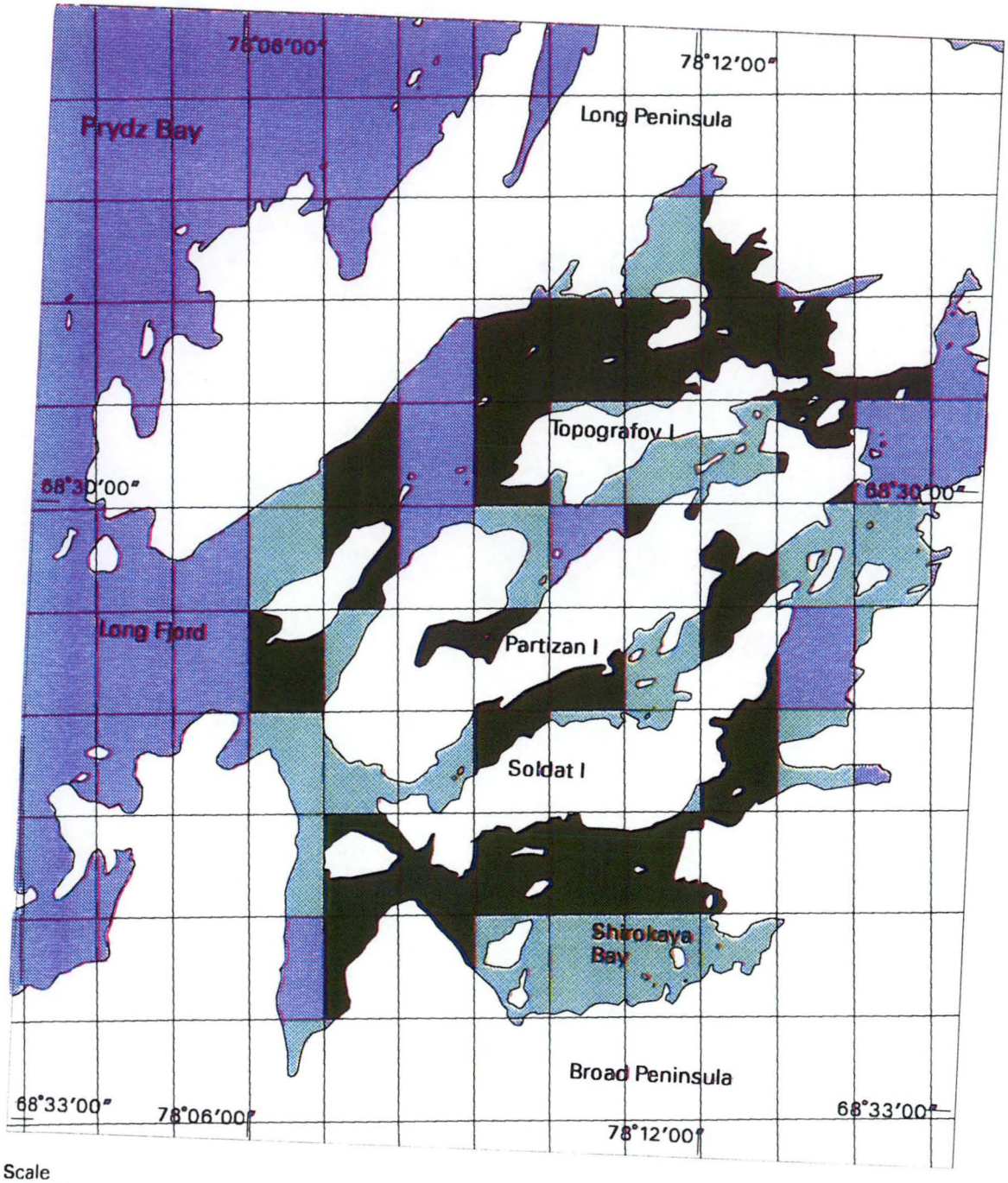


Fig. 3.6 Index of flooding associated with tide cracks

Key: Index = 4 Index = 5

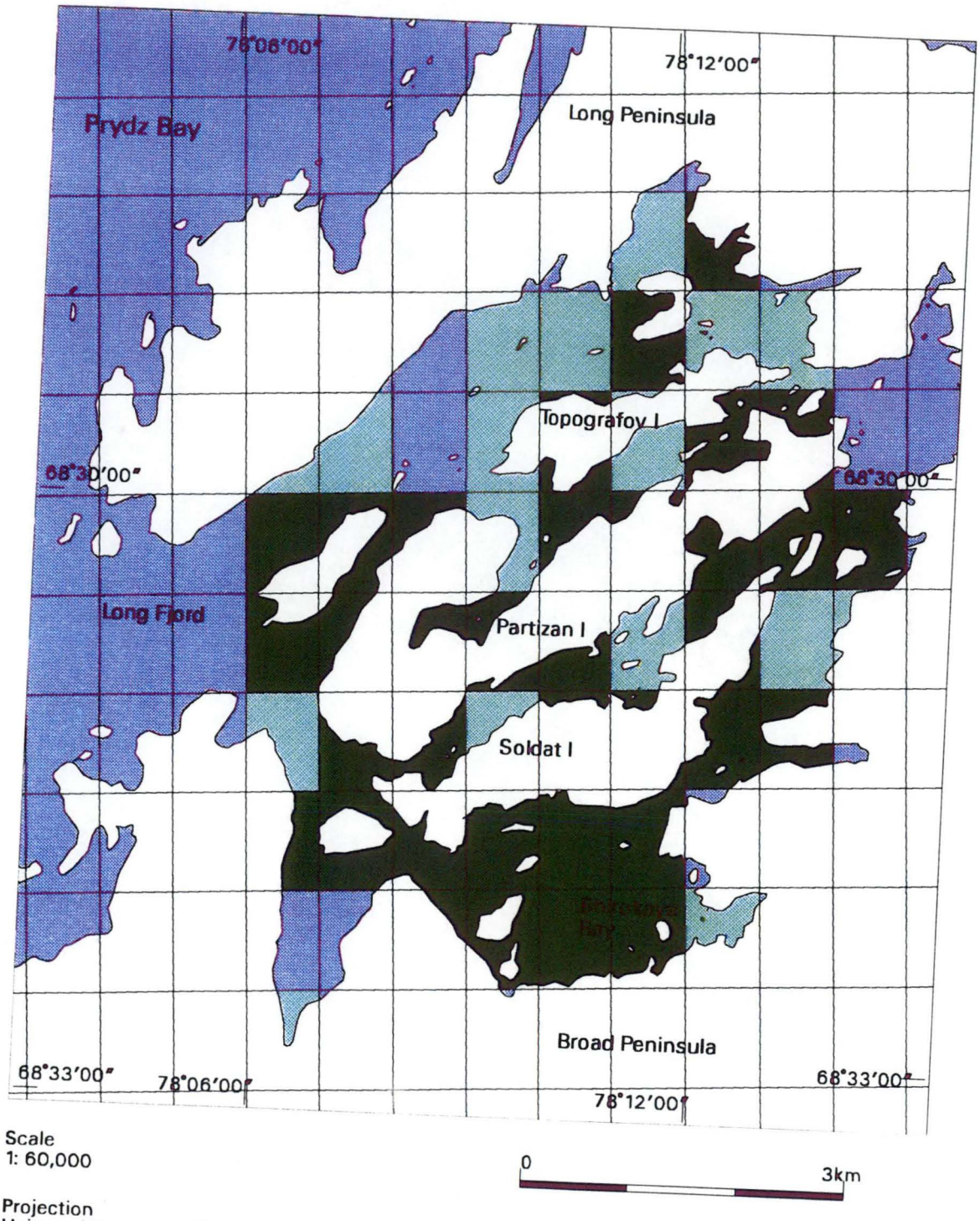


Fig. 3.7 Height of rafted ice associated with tide cracks

Key: 1 m 1 - 2 m

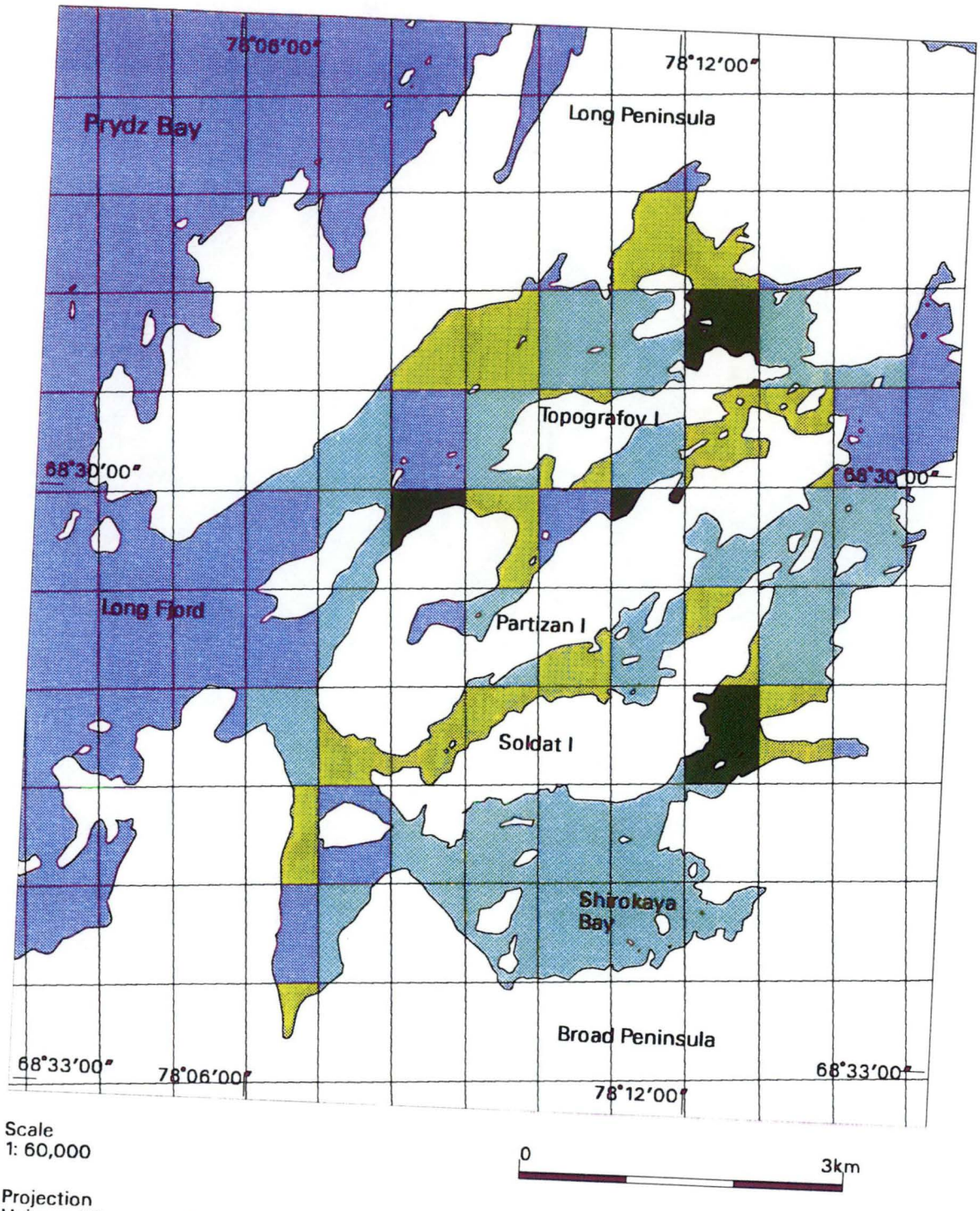


Fig. 3.8 Number of parallel cracks associated with tide cracks

Key: 4 cracks 5 cracks 6 cracks

Ice-structure

Tide-crack parameters were measured in grid squares where land was present (58 of 63 squares). Tests of multiple correlation were not significant which showed that the tide-crack parameters occurred independently of each other (df = 55: cracks/height r = 0.01, p = 0.91; pools/height r = 0.39, p = 0.11; pools/cracks r = 0.09, p = 0.45). There was no clear trend in the distribution of any parameter of ice-structure (Figs 3.5 - 3.7). Unlike the distribution of seals, the three parameters of ice-structure varied considerably in all four channels of the fjord and at both coastal and inshore areas within the study area (Figs 3.5 - 3.7).

Maximum values of ice-structure per grid square ranged between 3 and 7 cracks parallel to the coast (4.4 ± 0.8); 0.5 and 3 m high rafting (1.5 ± 0.5 m); and 1 and 5 for index of flooding (4.4 ± 0.8) (Fig 3.9). Most common were four cracks parallel to the coast, 1.5 m high rafting, and index 5 for pools. These characteristics of ice-structure occurred in about 50% of grid squares (Fig 3.9).

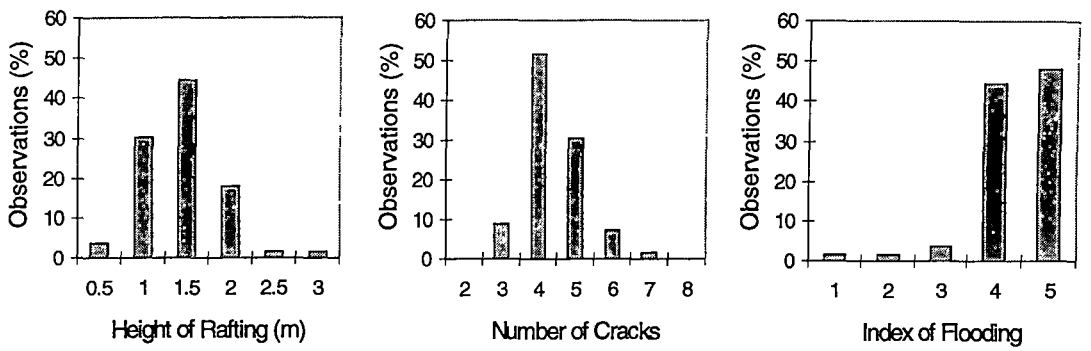


Fig 3.9 Percent frequency of categories in each parameter of tide-cracks. Height of rafting was maximum vertical height. Number of cracks was a count of cracks parallel to the shore. Index of flooding was a subjective scale from 1 - 5 where 1 was completely frozen and 5 was open water.

3.4 Discussion

Weddell seals aggregate in pupping colonies on the fast-ice in the spring. Several females share a single breathing hole and give birth between September and November on the sea-ice surrounding the hole (Ch. 1). Pups are suckled for about six weeks. During this time mothers and pups access the water through the breathing hole in the colony to swim intermittently (Tedman and Bryden 1979, Thomas and De Master 1983a). Males spend most of the time in the water beneath breathing holes where they defend aquatic territories against other males (Ray 1967, Bartish *et al.* 1992). The mature female ovulates early in December just before the pup is weaned. Underwater mating occurs then (Cline *et al.* 1971). This study includes sightings of 886 adults (28%) in addition to the assumed 2 319 adult females associated with pups. The extra adults are probably males (about 15%, Lake unpublished data) or non-pupping females present to mate with males. There is intraspecific competition for space and animals not involved in breeding activities are probably excluded from the breeding areas (Kooyman 1968, 1981, Stirling 1969a, 1974, Siniff *et al.* 1977, Croxall and Hiby 1983). Therefore distribution of animals in the study area conceptually is determined by the locations of breathing holes used by pupping females.

Weddell seals make breathing holes by enlarging existing cracks with their canine teeth (Stirling 1969a). Ice-cracks are created by tide which raises and lowers the level of the sea-ice (Ch. 1). The sea-ice is frozen to land or icebergs, and cracks form to make a hinge in the ice near the shore (Knox 1995). There are

ice-cracks around all the land and ice-bergs in tidal areas of fast-ice (S. Lake pers. obs.). Hypothetically pupping colonies could be located at any of these cracks. However, at McMurdo Sound (Stirling 1969a), Wilkes Land (Murray and Luders 1990) and the Vestfold Hills (this study) pups are not randomly distributed where there are tide-cracks. At McMurdo Sound and Wilkes Land the pups are concentrated in areas near a glacier tongue. The glacier causes the sea-ice to move (Ch. 1) which enlarges the tide-cracks, facilitating access to ice-surface for the seals. The reason for non-random distribution of seals at the Vestfold Hills is less apparent because breeding colonies are not in the vicinity of a glacier.

McMurdo Sound and Vestfold Hills are similar with regard to variability in the location of breeding seals (Stirling 1969b and this study). At McMurdo Sound variation in the location of breeding colonies is attributed to ice-structure. Females return to the same colony year after year but they will pup at adjacent sites should cracks not occur at the site normally used (Stirling 1969b). This suggests that sea-ice-structure is the ultimate determinant of the location of breeding colonies. In this study, ice-structure is quantified but the data are only preliminary. Sea-ice-structure varies between years (Stirling and Greenwood 1972) and this data about ice-structure is for one year only. Preliminary results suggest that sea-ice-structure is not the reason for non-random distribution of breeding seals. Tide-cracks in the channel occupied by seals have the same types of structure as tide-cracks in the three other channels (Figs 3.2 - 3.8). Thus while ice-structure accounts for variability in location of colonies it probably is not the reason for the non-random distribution of seals. To show this definitively it may

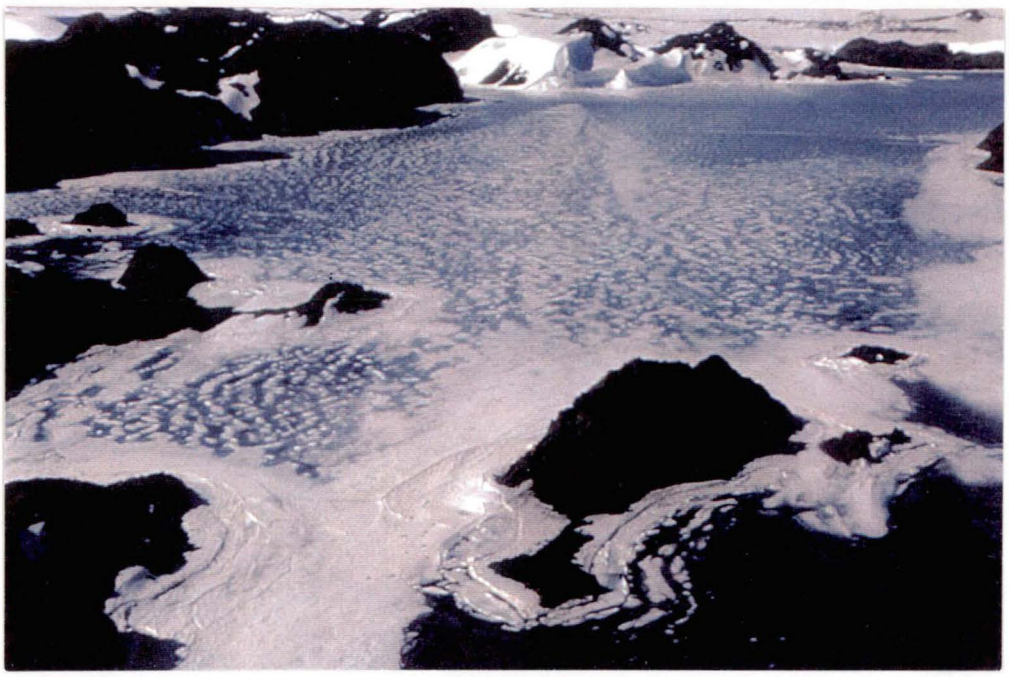
be necessary to refine the categories of ice-structure because one category of each parameter was recorded in up to 50% of grid-squares (Fig 3.9).

Other reasons for the non-random distribution Weddell seals could be social factors, availability of food, exposure to weather and predators, and stability of ice as breeding platforms (Stirling 1969a, 1971b, Testa and Siniff 1987, Ekau 1990). Currently it is not possible to evaluate these factors for Long Fjord due to the lack of data. Topography and weather have been described but there is no data for bathymetry, current flow, and distribution of prey. Regarding topography, three large islands in the study area divide Long Fjord into four channels. Channels between the islands are narrower than channels outside the islands. Seals are sighted mainly in the wide channels. Bathymetry and water current speed may vary with width of the channel. Seals would not be in shallow channels where the ice rests on the bottom at low tide. Further, current speed affects the distribution of prawns, *Chorismus antarcticus*, (Kirkwood and Burton 1988) which is an important prey species of Weddell seals at the Vestfold Hills (Ch. 4). It may be that Weddell seals occupy one channel where food is relatively abundant (Ekau 1990). In other areas, sea-ice stability and exposure to predators may be the reason for absence of seals. The northeastern channel is relatively exposed to the sea but not to wind (Burton and Campbell 1980). Like ringed seals (*Phoca hispida*) in the Arctic (McLaren 1958), complex coast is the optimum pupping habitat for Weddell seals because sea-ice is less likely to be blown away in areas of complex coastline (Stirling 1971b). Stable fast-ice provides Weddell seals with

platforms for breeding and protection from predators (Stirling 1969b, Testa and Siniff 1987).

At this stage, it is only possible to identify the types of factors that Weddell seals might respond to and emphasise the need for more research about the structure of Weddell seal habitat. Describing breeding habitat of Weddell seals is relevant to understanding ecosystem structure and function (as in Kooyman 1993) but the main reason for this study is for information to stratify surveys of population size. Future studies should focus on data that is available for broad areas. This could include topography, bathymetry and remote sensing of sea-ice.

Previous studies show that Weddell seal breeding colonies often occur in the vicinity of glaciers (Stirling 1969b, Murray and Luders 1990). This study shows that Weddell seal breeding colonies are not randomly distributed where they are not in the vicinity of glaciers. Both this and previous studies report interannual variation in the location of Weddell seal breeding colonies. The interannual variation shows that several years of data, from studies of long-term monitoring, are required to the describe distribution of breeding Weddell seals.



Aerial photograph of Long Fjord and west to the ice plateau

Chapter 4. Variation in Weddell seal diet

4.1 Introduction

Weddell seals are useful for collecting data about Antarctic coastal marine ecosystems because Weddell seals are predators at the top of that food web (Laws 1984). It is possible to integrate information about biochemistry, primary production and several layers of secondary production by measuring population parameters of higher-level predators (Trivelpiece *et al.* 1990). Population parameters of Weddell seals have been monitored at the Vestfold Hills since the 1973 and in latter years diet has been sampled concurrently with population monitoring. The population data show if there are fluctuations in the ecosystem (Testa *et al.* 1990). Diet information show how the predators interact with the ecosystem when the population parameters fluctuate (Green and Johnson 1988, Green *et al.* 1995). The success of such a study depends on accurate interannual comparisons of diet and thus identifying and controlling or correcting for variables. Seasonal variation in Weddell seal diet has already been established. The diet changes as the seals' distribution changes seasonally in synchrony with the extent of Antarctic fast-ice (Stirling 1969b, Green *et al.* 1987, Plötz 1986, Plötz *et al.* 1991). The present study examines fine-scale variation in Weddell seal diet to investigate the importance of sampling techniques for obtaining diet data that is comparable between years.

4.2 Methods

Diet

Individual faecal samples were collected and washed in a sieve of 0.25 mm mesh. Identifiable remains of prey were separated from other material in a sorting dish. Crustacean exoskeletons and cephalopod beaks were stored in Steedman's solution (Croxall 1993). Fish otoliths, vertebrae, jaw bones and eye lenses were stored dry. Other items such as amphipods, isopods, sand, rocks and seaweed were identified and their presence recorded on data sheets.

Analysis was of prey species, fish by habitat (benthic or pelagic) and general prey types. Abundance of prey remains was quantified by frequency of occurrence (the number of samples where remains occurred). Number of remains was also recorded. Prey species were detected by either left or right otoliths for fish, lower beaks for cephalopods and carapaces for prawns. Fish by habitat (benthic/pelagic) were quantified by either otoliths or vertebrae. Broad prey types were quantified by otoliths and vertebrae for fish, upper and lower beaks for cephalopods and carapaces for prawns. Similarly, other broad prey types were recorded as present if there was any evidence of that prey in the sample.

Otoliths were identified to species by reference to Williams and McEldowney (1990). Vertebrae were categorised as benthic or pelagic by reference to skeletal collections at the Australian Antarctic Division. Prawn species were identified to species by reference to Kirkwood (1984). Cephalopod taxa were identified by C. C. Lu (Victorian Museum). Measurements of fish otolith length were by digital image analysis (± 0.001 mm). Only otoliths showing slight or no sign of erosion were measured. Measurements of prawn carapace length and cephalopod beaks were by

vernier calliper (± 0.01 mm). Regression equations to estimate lengths and masses of prey were from Williams and McEldowney (1990) and Lu and Williams (1994). There were no regression equations for either octopus or prawns.

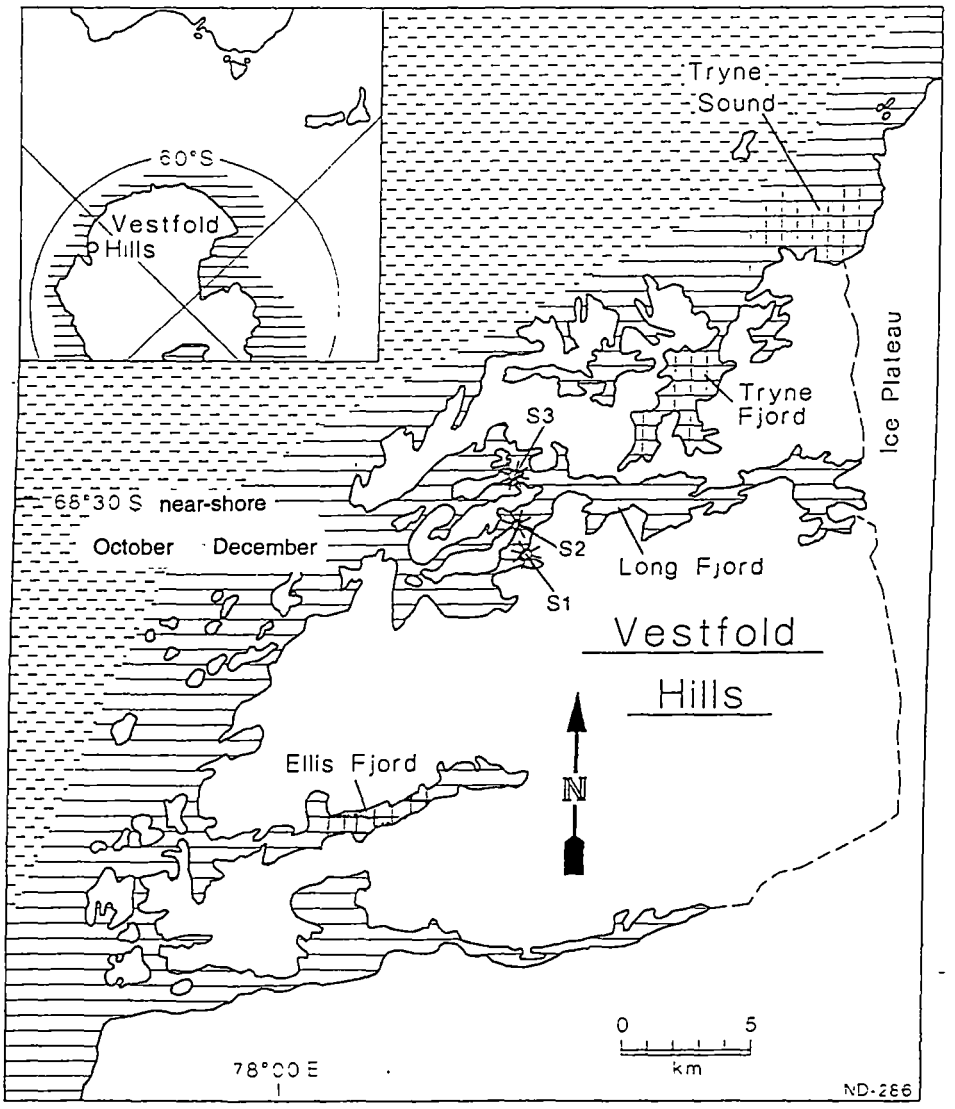


Fig 4.1 Faecal sample collection areas. In October samples were collected from sites (S) 1-3 and fast-ice near-shore (area of dashed lines). In December samples were collected from sites 1-3 and fast-ice near-shore but closer to the coast than in October (area of whole lines). In February samples were collected from Tryne Fjord, Tryne Sound and Ellis Fjord (area of crossed lines). These were the locations of seals at the time of sampling.

Analysis of variation in diet

Samples were collected every two months (11 - 25 October 1994, 9 - 15 December 1994 and 6 - 20 February 1995, Table 4.1). Collection areas in October were three breeding colonies (sites 1-3) in Long Fjord and a range of non-breeding sites on the fast-ice west of the Vestfold Hills (near-shore) (Fig 4.1). Collection areas in December were the same as in October (Table 4.1) except that sites near-shore were closer to the coast because the ice-edge had receded (Fig 4.1). In February the seals were concentrated at remnant sea-ice further north and also in Ellis Fjord. Samples were collected throughout these areas (Fig 4.1). Breeding colonies were occupied predominantly by adult females (pupping and not pupping). Other sites were occupied by non-pupping adults and juveniles of both sexes. Between 18 and 26 samples were analysed from each site (Table 4.1).

Table 4.1. Number and description of samples from each collection site and interval in 1994/5. Breeding colonies in Long Fjord (sites 1-3) were approximately 2 km apart. 'Near-shore' were non-breeding haul-out sites on the fast-ice west of the Vestfold Hills. Moulting seals in Tryne Fjord, Tryne Sound and Ellis Fjord were sampled in February

Collection site	Description	October	December	February
site 1 (Long Fjord)	breeding colony	18	18	.
site 2 " "	breeding colony	19	19	.
site 3 " "	breeding colony	20	18	.
near-shore	non-breeding	21	26	.
Long Fjord	non-breeding	.	8	.
Ellis Fjord	non-breeding	.	.	19
Tryne Fjord	non-breeding	.	.	20
Tryne Sound	non-breeding	.	.	18
Total	.	78	81	57

Diets at different sites and in different months were contrasted using the Mantel test procedures of PATN software (Belbin 1993). The Mantel test, a generalised regression approach to matrix correspondence, was used to compare the sum of cross-products of analogous cells in distance matrices against the null hypothesis of random permutations between rows and columns (Mantel 1967). The distance matrices were calculated using the Bray-Curtis index. One thousand permutations of equal sample sizes were made as recommended by Luo and Fox (1994). Significance was tested to probabilities of 0.05 which was downsized to probabilities of 0.1 to account for multiple comparisons and thus family-wise error rates. The data were frequency of occurrence expressed as a proportion of samples. The prey types were benthic fish, pelagic fish, octopus and prawns.

4.3 Results

From 216 samples, 463 fish otoliths, 3 898 fish vertebrae, 1 441 prawn exoskeletons and 81 cephalopod beaks were collected. Of these, 234 otoliths and 45 cephalopod beaks could not be identified because they were too digested or they were upper beaks. Thus one identifiable otolith and 0.2 identifiable squid beaks were recovered per sample. Ninety otoliths (19%) were measured.

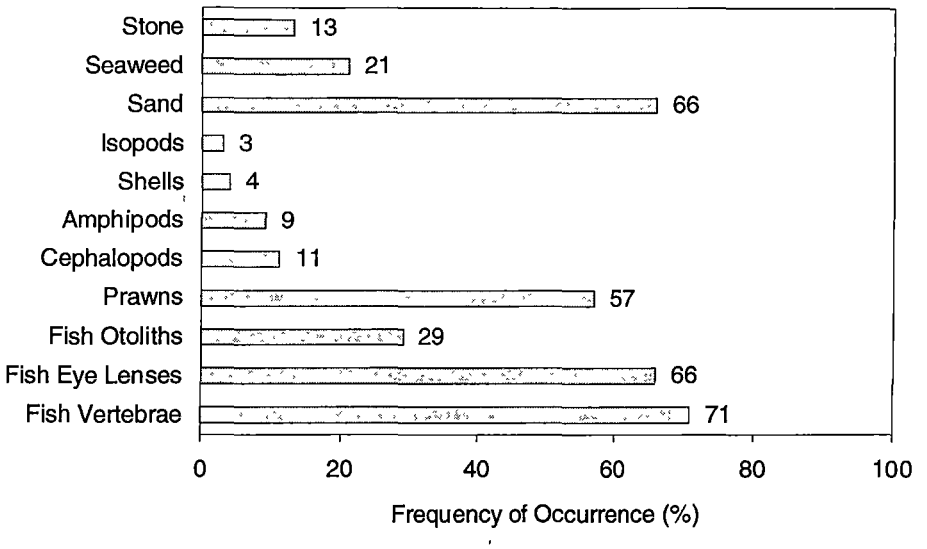


Fig 4.2 The proportion of samples (% frequency of occurrence) in which each type of prey remain was detected. Data were for all samples (n = 216). Shells were bivalve < 5 mm. Cephalopod remains were beaks. Prawn, amphipod and isopod remains were exoskeletons

Diet composition

A large proportion of samples contained fish otoliths (29%), fish vertebrae (71%) or prawn (decapod crustacean) exoskeletons (57%) (Fig 4.2). Fish, prawns and also cephalopods (11%) were the relatively large prey. Other identifiable fauna included amphipods (9%), isopods (3%) and gastropods (bivalve shells < 5 mm diameter, 4%). These relatively small fauna may have been ingested via the stomach contents of fish and cephalopods or as bycatch. They were insignificant in the diet by both frequency of occurrence and size. Sand, stone and seaweed occurred in many samples (Fig 4.2).

Fish remains (otoliths or vertebrae) were most common (74% of samples, Table 4.2). This included benthic fish (71%) such as *Trematomus scotti* (8%), *Pagothenia bernacchii* (5%) and *Pagothenia borchgrevinki* (2%) (Table 4.2). Two other benthic fish species (*Gymnodraco acuticeps* and an unidentified channichthyid) were in one sample each (< 1%). One pelagic fish species *Pleuragramma antarcticum*

Table 4.2 Prey species identified in the diet (n = 216 samples). Species were identified from otoliths, lower beaks or carapaces. Prey categories were quantified by other remains (as specified) in addition to species-specific remains. Quantification was by frequency of occurrence (FOO) and total number (NO) of prey remains (n = number of samples / remains)

Prey species	Family	Habitat	FOO		NO.	
			%	n	%	n
Trematomus scotti	Nototheniid	benthic	7.9	17	51	112
Pagothenia bernacchii	Nototheniid	benthic	4.6	10	13	29
Pagothenia borchgrevinki	Nototheniid	cryopelagic / benthic	2.3	5	3	7
Gymnodraco acuticeps	Bathydraconid	benthic	0.5	1	1	1
not identified	Channichthyid	benthic	0.5	1	1	1
Pleuragramma antarcticum	Nototheniid	pelagic	2.3	5	31	68
Fish (inc. vertebrae)			73.6	159	.	.
Psychroteuthis glacialis	Squid	bentho-pelagic	0.9	2	4	2
Pareledone harrissoni	Octopod	benthic	5.6	12	96	43
Cephalopods (inc. upper beaks)			12.0	26	.	81
Chorismus antarcticus	Decapod	benthic	54.6	118	95	1 366
Notocrangon antarcticus	Decapod	benthic	1.4	3	5	72
Prawns (total)			55.6	120	.	1 438

Table 4.3 Estimates of length and mass of individual prey estimated from measurements of otolith length, carapace length or lower-beak rostrum length. The data are mean ± standard deviation. Regression equations were not available for prawns or octopus. Number of items, and number of samples from which those items are derived, are shown

	Estimated size		Measurement	No. measured	
	Length mm	Mass g	Length mm	Items	Sample
Trematomus scotti	93 ± 17	12 ± 11	4.6 ± 0.7	27	3
Pagothenia borchgrevinki	194 ± 05	28 ± 15	2.9 ± 0.1	4	3
Pagothenia bernacchii	123 ± 23	125 ± 10	3.4 ± 0.4	18	5
Pleuragramma antarcticum	119 ± 36	16 ± 22	1.3 ± 0.3	38	8
Chorismus antarcticus	.	.	14.3 ± 1.7	727	73
Notocrangon antarcticus	.	.	13.6 ± 2.2	71	3
Psychroteuthis glacialis	147 ± 35	255 ± 35	4.45 ± 1.7	2	2
Pareledone harrissoni	.	.	13.6 ± 2.2	43	12

was evident (2% by otoliths, 7% by vertebrae). Both *T. scotti* and *P. antarcticum* were represented by relatively large numbers of otoliths per sample (7 ± 13 otoliths and 14 ± 19 otoliths respectively). These fish species were relatively small (93 ± 17 g and 119 ± 36 g respectively) compared to other fish species (Table 4.3).

Prawns were the second most important prey type by frequency of occurrence (56%) (Table 4.2). Most remains were from the benthic species *Chorismus antarcticus* (55%). Another benthic prawn species, *Notocrangon antarcticus,* was found in three samples (Table 4.2). *Chorismus antarcticus* was abundant per sample (12 ± 18 carapaces). Cephalopods were evident in 12% of samples (Table 4.2). The cephalopod species were predominantly octopus, *Pareledone harrissoni* (6%). Squid, *Psychroteuthis glacialis*, was in two samples.

Temporal variation

The Mantel test was used to contrast diets in October and December at the three breeding colonies that were repeatedly sampled. There was significant variation between months at every site (Table 4.4) probably due to changes in frequency of occurrence of benthic fish and prawns (Fig 4.3). The frequency of occurrence of benthic fish decreased from about 80% of samples in October, to 60% of samples in December and February (Fig 4.3). Similarly, frequency of occurrence of prawns decreased from about 70% of samples in October, to 50% of samples in December and February. By contrast, frequency of occurrence of pelagic fish increased from about 5% of samples in October and December to 15% of samples in February. Octopus was not part of the diet in February (Fig 4.3).

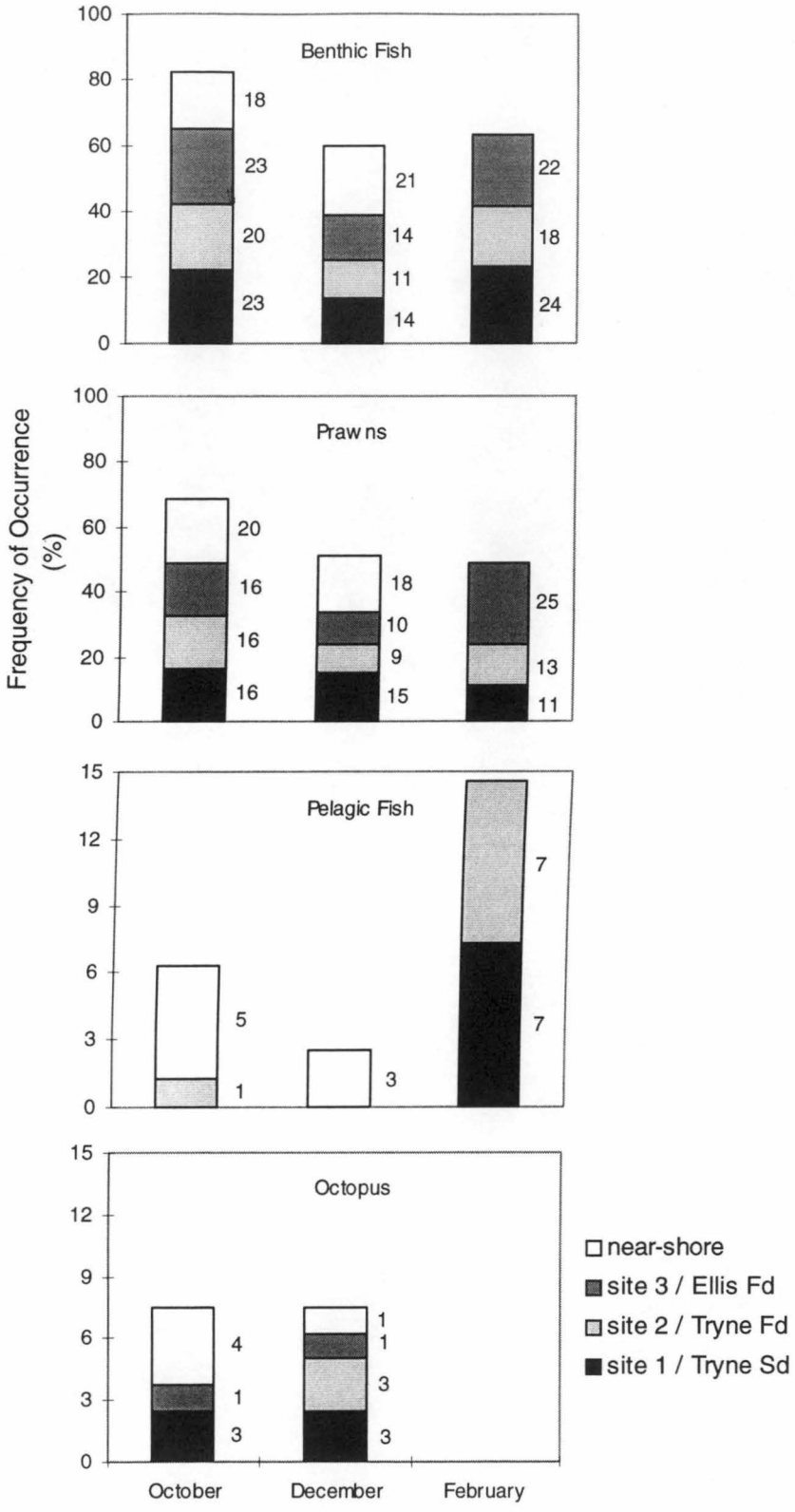


Fig 4.3 Temporal and spatial variation in frequency of occurrence of prey remains in samples. Near-shore and sites 1 - 3 were sampled in October and December. Ellis Fjord, Tryne Fjord and Tryne Sound were sampled in February. Values were the frequency of occurrence of each prey type from each site at each time samples were collected

Spatial variation

The Mantel test was also used to contrast diets between the various sites sampled at the same time. The variations were significant, especially in December and February (Table 4.4). During the breeding season the diet near-shore was similar to that within Long Fjord (Table 4.4). Pelagic fish occurred almost exclusively in samples from near-shore but the frequency of occurrence was low and the frequencies of occurrence of benthic fish, octopus and prawns in samples from near-shore were similar to those at sites in Long Fjord (Fig 4.3). During the moulting season the frequency of occurrence of prawns was much higher in samples from Ellis Fjord than in samples from Tryne Fjord and Tryne Bay. Conversely, pelagic fish was in samples from Tryne Fjord and Tryne Bay but not in samples from Ellis Fjord. Both benthic and pelagic fish were in more samples from Tryne Sound than Tryne Fjord (Fig 4.3).

Table 4.4 Mantel tests of significance of temporal and spatial variation ($p < 0.1$ shown as *). Sites 1 - 3 were breeding colonies in Long Fjord. 'Near-shore' were non-breeding seals on fast-ice west of the Vestfold Hills. Ellis Fd, Tryne Fd and Tryne Sd were moulting seals

Comparison		Site 1		Site 2		Site 3	
October	December	0.023	*	0.032	*	0.019	*
		October		December		February	
site 1	site 2	0.10		0.57		.	
site 1	site 3	0.05		< 0.01	*	.	
site 1	near-shore	0.78		0.06		.	
site 2	site 3	< 0.01	*	0.02	*	.	
site 2	near-shore	0.1		0.03	*	.	
site 3	near-shore	0.1		0.04	*	.	
Ellis Fd	Tryne Fd	.		.		0.01	*
Tryne Fd	Tryne Sd	.		.		0.01	*
Tryne Sd	Ellis Fd	.		.		0.01	*

4.4 Discussion

The results of this study are fundamental to making comparative studies of Weddell seal diet because they show the fine-scale temporal and spatial variation of diet within a sample collection area (Vestfold Hills) and thus the potential for sampling bias if not controlled or corrected for in the methods for comparison of diet.

Faecal sample analysis

In this study, one identifiable otolith and 0.2 identifiable cephalopod beaks were recovered on average per sample. Low recovery rates of otoliths were also reported by Testa *et al.* (1985) who found no otoliths in 32 faecal samples from Weddell seals at McMurdo Sound. By contrast, Weddell seal stomach samples contained high numbers of species-specific remains eg. 16 otoliths (Gales and Burton 1988), 372 otoliths (Plötz 1986), and 100 otoliths (Plötz *et al.* 1991) per stomach sample; 3 lower beaks (Gales and Burton 1988), 4.5 lower beaks (Plötz 1988), 1.9 lower beaks (Plötz *et al.* 1991), 79.0 lower beaks (Clarke and Macleod 1982) and 5.9 lower beaks (Lipinski and Woyciechowski 1981) per stomach sample. The difference in recovery rates between faecal and stomach samples indicated that species-specific remains were digested in the Weddell seal intestine. Further, it indicated that the number of species-specific prey remains in faeces was not indicative of the number of prey consumed.

Many stomach samples could not be obtained from Weddell seals because lethal methods (used by Plötz 1988, Plötz *et al.* 1991, Clarke and Macleod 1982, Lipinski and Woyciechowski 1981) were inappropriate for this study, anaesthetics placed the seals' life at risk (Gales 1989) and emetics were ineffective (Bornemann *et*

al. 1997). However, Green and Burton (1987) showed that all types of prey remains in stomach samples, and more, were represented in faeces when many samples were analysed. In this study, the prey remains recovered from faeces were not often species-specific but they were usually suitable for quantification to broad prey categories. The numbers of remains in samples were not comparable between categories because recovery rates would have varied between exoskeletons and beaks, for example (Croxall 1993). Thus analysis of faecal samples was limited to frequency of occurrence for broad prey categories. Species identifications were to describe composition of diet only.

Composition of diet

Benthic fish (71%) and prawns (56%) were the main components of Weddell seal diet. Pelagic fish (7%) and cephalopods (12%) also occurred in the diet but less frequently. The general description of diet was consistent with previous studies of the summer diet of Weddell seals at the Vestfold Hills (Green and Burton 1987, Green *et al.* 1993). Apparently the diet was specific to the Vestfold Hills, especially with regard to the importance of prawns. At McMurdo Sound, Weddell seals fed primarily on pelagic fish (Dearborn 1965, Kooyman 1981, Testa *et al.* 1985). At the Antarctic Peninsula, Weddell seals fed primarily on cephalopods (Lipinski and Woyciechowski 1981, Clarke and Macleod 1982). Pelagic and benthic fish were the main components of diet in the Weddell Sea (Plötz 1988, Plötz *et al.* 1991). Thus the diet of Weddell seals generally has consisted of benthic fish, pelagic fish, prawns and cephalopods but proportions of these prey in the diet has varied around Antarctica.

Prey species identified in this study included *Trematomus scotti* - a common inshore benthic species (Williams and McEldowney 1990), *Pagothenia bernacchii* - abundant in shallow (< 20 m deep), weedy and rocky habitats (Williams 1988), *Pagothenia borchgrevinki* - from specialised habitat associated with the underside of the sea-ice (Williams 1988) and *Pleuragramma antarcticum* - pelagic and ubiquitous over the continental shelf. The absence of fish species such as *Chionodraco hamatus* and *Pagothenia hansoni* (Williams 1988, Williams and Duhamel 1994) suggested that the prey were consumed from coastal areas. However prey from off-shore could have been excreted in transit to near-shore collection areas. Prawns were mainly (95%) *Chorismus antarcticus* - the shallowest-occurring (15 - 300 m) of two benthic prawn species in the ecosystem (Zarenkov 1970) and recorded in densities up to 20 per square metre (Kirkwood and Burton 1988). The high frequency of occurrence of *C. antarcticus*, body size up to 10 cm long (Clarke and Lakhani 1979, Kirkwood 1984) and the relative abundance of remains (12 ± 18 carapaces per sample) suggested that *C. antarcticus* was the most important, single-species in the diet. Cephalopods were predominantly octopus, *Pareledone harrissoni,* which has a mantle length of up to 10 cm (Lu and Stranks 1994). Green and Burton (1987) showed that Weddell seals at the Vestfold Hills took octopus near-shore in summer and consumed squid, *Psychroteuthis glacialis*, when they moved off-shore to deeper waters in winter.

There were two clear differences in species composition of the diet between this and previous studies at the Vestfold Hills (Green and Burton 1987, Green *et al.* 1993). These were 1). consumption of *Trematomus scotti* and 2). lack of consumption of *Notocrangon antarcticus*. Both species occurred in relatively deep, benthic habitat (> 200 m Zarenkov 1970, Williams 1988). *Trematomus scotti* has not

previously been shown in the diet of other Antarctic vertebrates despite being a common part of the fish fauna (Williams and McEldowney 1990, Plötz *et al.* 1991). The estimated individual mass of *T. scotti* in the diet was 12 g - less than half the estimated mass of other benthic fish species (Table 4.3). Other small fish prey (*P. antarcticum* 16 g) have been commonly consumed (eg. Plötz 1987, Testa *et al.* 1991, Green *et al.* 1993). However, *P. antarcticum* was pelagic and schooling and so probably easier to capture than foraging deep amongst the benthos for *T. scotti.* It was unlikely that *T. scotti* was secondarily ingested because the frequency of occurrence of *T. scotti* otoliths was higher than other fish species (Table 4.2). With regard to *N. antarcticus*, in previous years this prawn was consumed in quantities similar to *C. antarcticus* (Green and Burton 1987, Green *et al.* 1995). In this study it was in only three samples perhaps reflecting low availability of the species in this year.

Variation in diet

The interseasonal change in the diet of seals in Long Fjord suggested that prey stocks were locally depleted over time. The frequency of occurrence of both benthic fish and prawns decreased in diets at Long Fjord from 80% in October to 60% in December (Fig 4.3). The majority of seals in Long Fjord were breeding and the samples were from breeding colonies. The high frequency of occurrence of prey remains in samples and apparent depletion of fish stocks in Long Fjord indicated that breeding seals did feed during the breeding season. This inference was based on circumstantial evidence (faecal samples from unknown animals). However, Testa *et al.* (1985) showed by measuring prey abundance concurrently with dietary study that stocks were depleted over time when Weddell seals inhabited an area. Ekau (1990) showed that Weddell

seal breeding colonies were in areas of relatively dense prey (> 1 t. km^{-2}). Weddell seals ate an estimated 18 kg per day (Oritsland 1977). Therefore each square kilometre would provide approximately 55 Weddell seal foraging days. There were about 100 Weddell seals in 10 km of Long Fjord for three months (unpublished data) so prey-stock depletion was to be expected.

Implications for sampling

Spatial differences within the Vestfold Hills were most pronounced in December and February. The significance of differences between sites in these months indicated that the description of diet would have varied according to when and where samples were collected. In February, for example, pelagic fish were not evident in samples from Ellis Fjord and the frequency of occurrence of prawns in samples from Ellis Fjord was relatively high. Benthic fish were more abundant in samples from Tryne Sound than Tryne Fjord. Therefore the proportion of samples from each site determined the frequency of occurrence of prey described as the diet. Understanding this type of variation is critical for making interannual comparisons of diet because benthic fish, pelagic fish and prawns have repeatedly been shown to be the main components of Weddell seal diet at the Vestfold Hills, and the proportions of these components has varied between years (Green *et al.* 1993). This study shows that controlling for temporal and spatial variation within years in the frequency of occurrence of broad prey items is necessary to demonstrate and understand interannual differences in Weddell seal diet.

The Vestfold Hills, Prydz Bay, Antarctica

Chapter 5. Discussion

5.1 Introduction

This thesis consists of investigations of aspects of the biotic and abiotic environment which influence the distribution and abundance of Weddell seals. Weddell seals inhabit coastal areas of Antarctica where fast-ice provides almost complete surface cover over the ocean (Ch. 1). Distribution and abundance of tagged Weddell seals are monitored annually at the Vestfold Hills. Knowledge of variation within each year of data is important to make precise, interannual comparisons and thus describe the effects of variation in ecosystem conditions (Croxall 1989). Weddell seals have not been exploited (Siniff 1991) and the natural ecosystem events that Weddell seals respond to are of interest in themselves and relevant to modelling the effects of anthropogenic change such as fishing (Williams 1985).

5.2 Diurnal variation in haul-out

Most population assessments are indices of population size. To estimate absolute population size from counts of animals some thorough studies of behaviour over daily, seasonal, tidal, lunar, weather and life cycles are needed (Trillmich 1993). Chapter 2 is a description of daily and seasonal behaviours. A

diurnal pattern of haul-out activity is shown that is similar at various locations around the Antarctic continent (Siniff *et al.* 1971, Tedman and Bryden 1979, Thomas and DeMaster 1983a, Reijnders *et al.* 1990). Maximum numbers of seals are on the ice in the afternoon between about 1200 hours and 1700 hours. Diurnal variation in sightability of seals is much less in the breeding season (29%) than the moulting season (95%). This is because cows with newborn pups remain on the ice constantly (Thomas and DeMaster 1983a), and probably also because temperatures at the end of the moulting season are colder and seal behaviour is intermediate between summer (when they bask on the ice) and winter (when they mostly remain in the water).

It is discussed how knowledge of diurnal activity is relevant to maximising the number of resights of adult seals and that this, in addition to pup tagging, is the basis of Weddell seal long-term monitoring. Resight data are required for biological evidence of fluctuations in Antarctic ecosystems. For example, fluctuations in reproductive rate correlate with meteorological phenomena such as the SOI (Southern Oscillation Index, Testa et al. 1991) or the ACW (White and Peterson 1996, http://www.nbi. ac.uk./psmsl/gb3/jacobs.html, Ch. 1). Survivorship is also calculated as an index of interannual variation. Unlike reproductive data, survivorship data is based on resights of both breeding and non-breeding seals, and collecting survivorship data will be more efficient with knowledge of diurnal haul-out patterns in the local area.

5.3 Variation in abundance

Changes in population size are the ultimate result of changes in population parameters (DeLong *et al.* 1991). However, population size is relatively difficult to quantify and current estimates have low precision (Siniff *et al.* 1970, Erickson and Hanson 1990). Most studies of Weddell seals are at specific sites eg. Vestfold Hills or McMurdo Sound. The relative abundance of animals suggests that these are preferred breeding areas. Despite the reported high site fidelity of pinnipeds, shifts among habitats of differing quality have been documented for several species. In northern elephants seals, for example, about 32% of juvenile females give birth away from their own birth site (LeBoeuf and Reiter 1988). Apparently dominant animals fill the best habitat first and less competitive (young) individuals settle elsewhere (Trillmich 1993). Thus estimates of population size in good habitat (where researchers tend to make their observations) will underestimate impact of events (Trillmich 1993).

In this thesis, the preferred breeding habitat of Weddell seals at the Vestfold Hills is described with regard making regional estimates of population abundance. Chapter 3 includes an analysis of Weddell seal distribution in the most populated area at the Vestfold Hills. The data show that distribution of seals is not random and varies between years. Preliminary data to investigate the effect of ice-structure on the distribution of colonies are reported. The aim is to describe the most important or limiting aspects of habitat for seals in the breeding season. The knowledge is needed to stratify surveys of abundance and also to understand the Vestfold Hills study area in perspective of the range of potential habitat.

5.4 Variation in summer diet

When relating seal population changes to changes in diet, it should be considered that the diet at the Vestfold Hills is not necessarily from the marked animals whose demographic parameters are monitored. Many of the seals at the Vestfold Hills during the breeding season are not in the study area during the moulting season and vice versa (S. Lake pers. obs., H. Burton unpublished data). Further, the diet data in this work is for the summer only and Weddell seals obtain much of their nutrition during winter (Wilson 1907, Schreer and Testa 1996). Therefore the description of summer diet can be used as a comparative index of ecosystem conditions and cannot be used as a complete description of prey consumption.

Chapter 4 describes variation in the diet of Weddell seals. It shows significant temporal and spatial variations within the summer diet of Weddell seals at the Vestfold Hills. This suggests that a sampling protocol is required to control for variation within years in Weddell seal diet. There also is processed data for summer diet in four years of the 1980's (Green et al. 1993) and there are unprocessed samples from every year to date during the 1990's (Burton pers. comm). The evidence in Chapter 4 shows that it is necessary to check for temporal and spatial bias in this data before making comparisons between years.

A sampling protocol to control for spatial variation might include faecal samples collected in proportions similar to the proportion of seals in an area. For existing faecal collections, it may be necessary to compare seal distributions with collection areas and weight the sub-collections according to number of animals in the area. If faecal samples are taken regularly to control for temporal variation

then samples can be excluded after collection if the months of collection differ between years. The issue of sample size needs to be addressed. The required sample size can be calculated from the amount of difference in the diet required to show changes in the ecosystem.

5.5 Conclusions

It is far from a trivial matter to determine changes in pinniped populations. The number of seals on top of the ice varies considerably, and if counts of seals are to be used as an index of population size then factors that affect the proportions of seals on the ice and in the water need to be controlled or corrected for. This thesis reports diurnal variation in numbers of seals and how this changes seasonally (Ch. 2), but there are other variables that also need to be considered such as tidal and lunar cycles. The ultimate effect of changes in population parameters is population increase or decrease. Surveys of population size need to be on a regional scale. Weddell seals are not randomly distributed (Ch. 3). It would be more efficient to know where seals are abundant and survey those areas intensely. At this stage, aspects of habitat that determine Weddell seal abundance are not known and more research is required to be able to predict the locations of concentrations of Weddell seals. Interannual variation in diet provides useful information for inferring the reasons for population fluctuations and modelling the impacts of man. Chapter 4 is an investigation and discussion of how to collect

samples to represent Weddell seal diet more accurately. Improved methods will assist comparisons of diet between years in showing real differences in prey type that can be used as an index of ecosystem conditions. Combined with data to increase the precision of censuses, and the study of Weddell seal distribution, the investigations in this thesis make both technical and biological contributions to population monitoring of Weddell seals at the Vestfold Hills.

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